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HILLTOPPING

AN ECOLOGICAL STUDY OF SUMMIT CONGREGATION BEHAVIOR OF BUTTERFLIES ON A SOUTHERN CALIFORNIA HILL

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FOREWORD

"Territoriality" in various vertebrate animals has been studied for many years, involving not only the fact that territoriality exists as a behavior pattern but also involving a functional need for this behavior in the life history of the animal. "Hilltopping" of butterflies as a form of territoriality has been observed by all persons who have collected, or studied, these invertebrates in the field, but no one has made such a concerted effort at obtaining analytical data as has Mr. Oakley Shields. All experimental and/or analytical studies represent an effort on the part of a worker at obtaining significant data upon which to draw conclusions; there are apt to be as many different conclusions derived from the same set of data as there are independent analyses made of them but we can be sure that Mr. Shields has made every effort at drawing conclusions in keeping with the data he has presented. Others may be able to draw other conclusions from the same data. This is in the fulfillment of scientific spirit, and is as it should be. Mr. Shields has also given a very complete Bibliography of work related to this field. The literature of entomology is extremely large and he is to be commended for his efforts; such omissions as have occurred should be considered in the context that it could happen to any of us.

The Lepidoptera Research Foundation, Inc. *is proud to be able to present this work of Mr. Oakley Shields in complete form in the thought that in this way it will prove to be more usable and satisfactory than if it were divided into sections for publication.*

William Hovanitz
Editor

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ABSTRACT

It is widely known that butterflies often congregate in numbers on the summits of hills, ridges, peaks, and mountain-tops. However, few investigations have been made to determine why this behavior has developed. This study was conducted to try to answer this question.

Initially, purely observational work was necessary to adequately describe the phenomenon. Dictionary Hill near Spring Valley, San Diego County, California, was chosen as the primary study area because it was readily accessible and the surrounding area was relatively undisturbed by man. To follow the behavior of individuals, a mark-release program was established. It was

found that the summit population consisted primarily of males that exhibited territorial or pathway-patrol behavior, with aggression displayed toward other butterflies. These males sometimes spent most of the day in such behavior and repeatedly returned to the summit on subsequent days. During the study 21 species were found to congregate on the summit, while another 25 species flew "up-and-over" the summit without congregating or were generally distributed over the entire hill.

Certain insects are known to congregate at topographic summits to facilitate mating. To test this hypothesis for butterflies, the behavior of females that approached the summit was observed and females were collected. An abnormally high percentage of females captured on the summit was virgin when compared to those captured elsewhere. This fact was determined by the absence of a spermatophore in the female's bursa copulatrix. Also, a substantial number of summit matings was observed for two species on the summit. The apparent scarcity of females was due to the inconspicuousness of *in copula* pairs and due to the fact that virgins stayed only long enough to mate and non-virgins only rarely approached the summit. Virgin females lingered about the summit until mated and readily mated with courting males. Females of two species were seen to depart from the summit after mating.

Further evidence that this phenomenon serves to bring males and females together to insure fertilization comes from an experiment in which mated and unmated females of one species, *Papilio zelicaon*, were released away from the hill. Only the unmated females were later captured on the summit, indicating that virgin females seek the summit. Evidence that males actively seek the summit comes from the fact that a substantial number of male *P. zelicaon* released at various directions and distances away from the hill later returned to the summit.

The evidence strongly indicates that "hilltopping" in butterflies is a phenomenon in which males and virgin (or multiple-mating) females instinctively seek a topographic summit to mate. The selective advantage presumably would be to centralize isolated populations for mating and thus stabilize the gene pool. Other possible alternative explanations have been advanced in the literature but all are here shown to be highly unlikely. The strongest alternative theory, that butterflies are concentrated on summits due to winds and updrafts, is shown to be unsatisfactory.

Observations on feeding, roosting, and predation of hilltopping butterflies are also included, and the phenomenon is discussed in relation to hilltopping insects.

INTRODUCTION

Students of insect behavior are aware that insects are largely at the mercy of their instincts. Insects do not behave a certain way because it is fun or because they want to but do so because their instincts compel them to. Thus when one sees butterfles flying about the summit of a hill and "playing tag" with each other, one may wonder what instinct brought them there and why the habit developed. This study was conducted to determine the reasons for this summit congregation behavior in butterflies.

Swarms of insects on the summits of ridges, hills, and mountains are frequently mentioned in the literature (Slosson, 1893, 1894, 1895; Bowditch, 1896; Guppy, 1897; Newcomb, 1901; Currie, 1904; Poulton, 1904; Hudson, 1905; Meinecke, 1917; Howard, 1918; Van Dyke, 1919; Bryan, 1923, 1926; Scott, 1926; Swezey and Williams, 1932; Alexander, 1940; Chapman, 1954a; Edwards, 1956, 1957b, 1960, 1961; Mani, 1962). Sometimes large numbers of different insects are found dead on snow at summits (Bowditch, 1896; Caudell, 1903; Currie, 1904; Bryan, 1917, 1923; Meinecke, 1917; Fletcher, 1964:141). Such swarms are often composed almost entirely or exclusively of males that are congregating on a prominence from the surrounding territory (see, for example, Chapman, 1954a; Dodge & Seago, 1954; Catts, 1964; Shepard, 1966). Groups frequenting summits include the orders Coleoptera, Diptera, Hymenoptera, and Lepidoptera (Table 1). A number of Lepidoptera families contain species that show

TABLE 1. Families of insects with species that are known to hilltop

Family	Sources
COLEOPTERA	
Byrrhidae	Edwards, 1956
Cerambycidae	Poulton, 1904
Chysomelidae	Slosson, 1893; Van Dyke, 1919
Coccinellidae	Slosson, 1893; Poulton, 1904; Hudson, 1905; Van Dyke, 1919; Bryan, 1926; Balduf, 1935; Chapman, 1954a; Chapman, Romer, and Stark, 1955; Edwards, 1956, 1957a; Hagen, 1962
Elateridae	Edwards, 1956
Scarabaeidae	Hudson, 1905
Rhynchophora	Van Dyke, 1919
DIPTERA	
Agromyzidae	Bryan, 1926
Anthomyidae	Bryan, 1926
Bibionidae	Hudson, 1905
Bombyliidae	Currie, 1904; Van Dyke, 1919; Chapman, 1954a; Dodge and Seago, 1954; Edwards, 1956, 1957b
Borboridae	Bryan, 1926
Calliphoridae	Dodge and Seago, 1954; Edwards, 1956
Culicidae	Knab, 1907
Cuterebridae	Chapman, 1954a; Catts, 1963
Gastrophilidae	Walton, 1930; Grunin, 1959
Hypodermatidae	Grunin, 1959
Muscidae	Bryan, 1926; Scott, 1926; Dodge and Seago, 1954; Edwards, 1957b
Oestridae	Aldrich, 1915; Grunin, 1959; Catts 1964
Phoridae	Dodge and Seago, 1954
Rhagionidae	Shemanchuk and Weintraub, 1961
Sarcophagidae	Chapman, 1954a; Dodge and Seago, 1954; Edwards, 1956, 1957b; Grunin, 1959
Simuliidae	Edwards, 1956
Syrphidae	Currie, 1904; Van Dyke, 1919; Bryan, 1926; Chapman, 1954a; Dodge and Seago, 1954; Edwards, 1956, 1960
Tabanidae	Chapman, 1954a; Dodge and Seago, 1954; Edwards, 1956, 1957b
Tachinidae	Currie, 1904; Van Dyke, 1919; Bryan, 1926; Chapman, 1954a; Edwards, 1956, 1960
HYMENOPTERA	
Formicidae (winged ants only)	Poulton, 1904; Hudson, 1905; Wheeler, 1905, 1917a; Van Dyke, 1919; Scott, 1926; Gregg, 1947; Michener, 1948; Chapman, 1954b; Fosberg, 1955; Chapman, 1957
Ichneumonidae	Slosson, 1894; Bryan, 1926; Chapman, 1954a
Psammocharidae	Bryan, 1926
Siricidae	Scott, 1923, 1924, 1926; Walsh, 1924; Chapman, 1954a; Edwards, 1957b
Sphecidae	Poulton, 1904

hilltopping activity: Hesperiidae, Lycaenidae, Nymphalidae, Papilionidae, and Pieridae (Table 2). Welling (1958) reported the phenomenon in some nocturnal moths on a hill in Ohio. Certain hibernating Coccinellidae, Chrysomelidae, and Rhynchophora beetle aggregations (Van Dyke, 1919; Chapman, 1954a) and aestivating Noctuidae moth aggregations (Common, 1952) have been reported from summits; such aggregations were not composed predominantly of males. The explanation of this phenomenon of insects congregating on summits, known as "hilltopping" in butterfly literature, is known for certain insects but remains unsettled for butterflies.

Butterfly collectors often find that hilltops are profitable places to collect. Certain species that are rare or apparently absent in the surrounding countryside may congregate at such places in numbers (Van Someren, 1955). Barrett and Burns (1951:4-5), in referring to males of many species of hesperiids and lycaenids in Australia and New Guinea, said that certain hilltops will always have particular species at the proper time of year. Knudsen (1954) found three species of butterflies abundant on Kennesaw Mountain, Georgia. Here he found on the summit several hundred butterflies in an area of a few hundred square feet. On two hilltops in Australia, Waterhouse (1932:267) found butterflies clustered by the hundreds just before dusk or on the lee side of a shrub during wind. Minimum distances traveled by hilltopping butterflies from the nearest areas of their foodplants are reported as several thousand vertical feet for *Papilio indra kaibabensis* in Arizona (Emmel & Emmel, 1967) and 1,700 vertical meters for *Pieris callidice* in France (Muspratt, 1954).

Various theories have been proposed for hilltopping among insects. Poulton (1904) discussed insects in general that frequent summits and concluded that they seek "conspicuous isolated features in the landscape" to mate, thus greatly reducing the area in which sexual encounters could occur. He offered as supporting evidence the ceramycid *Dorcadion* "pairing freely" on a summit. This theory has been particularly substantiated by work with winged ants and bot flies: observations by Forel (1874), Michener (1948), Fosberg (1955), and Chapman (1957) refer to matings among summit swarms of winged ants; bot flies on summits were reported to mate by Walton (1930), Grunin (1959), and Catts (1963, 1964). Dodge and Seago (1954) reported twenty-one mating pairs of Diptera from mountain summits of Georgia, and Chapman (1954a) mentioned

TABLE 2. A list of known butterfly "hilltopping" species

Species	Realm	Sources
PAPILIONIDAE		
Papilioninae		
Battus philenor	Nea.	Weiss, 1927; Merritt, 1952
B. polydamus	Neo.	new (Brown)
Chilasa clytia	Ori.	Tinkham, 1937; Best, 1954; Wynter-Blyth, 1957
C. c. dissimilis	Ori.	Best, 1954
Graphium, most spec.	Neo.	new (Brown)
G. marcellus	Nea.	Merritt, 1952; Knudsen 1954
Papilio, many spec.	Neo.	new (Brown)
P. anactus	Aus.	new (Wyatt)
P. anchisiades	Neo.	new (Brown)
P. androgeus	Neo.	new (Brown)
P. angolanus	Eth.	Van Someren, 1955
P. arcturus	Ori.	Wynter-Blyth, 1957
P. bairdii	Nea.	Grinnell and Grinnell, 1907 new (many)
P. b. brucei	Nea.	Rodeck, 1950; Newcomer, 1967
P. brevicauda	Nea.	Edwards, 1884; Tilden, 1964
P. crino	Ori.	Best, 1954
P. demodocus	Eth.	Longstaff, 1912:225; Van Someren, 1955
P. demoleus	Eth.	Trimen, 1889
P. eurymedon	Nea.	Edwards, 1887; Merritt, 1952; Garth and Tilden, 1963
P. feisthamelii	Pal.	new (Wyatt)
P. glaucus	Nea.	Scudder, 1887, 1889; Weed, 1901; Longstaff, 1912: 149; Weiss, 1927; Merritt, 1952
P. g. arcticus	Nea.	Wyatt, 1957a
P. hector	Ori.	Longstaff, 1912: 380
P. indra	Nea.	Mead, 1878; Edwards, 1884; Wright, 1906; Newcomer, 1910; Martin and Ingham, 1930; Garth, 1934; Emmel and Emmel, 1962; Garth and Tilden, 1963
P. indra fordi	Nea.	new (many)
P. i. kaibabensis	Nea.	Emmel and Emmel, 1967
P. i. martini	Nea.	Emmel and Emmel, 1968
P. i. minori	Nea.	Eff, 1962
P. i. pergamus	Nea.	new (many)

TABLE 2 (continued)

Species	Realm	Sources
Papilio leonidas	Eth.	Van Someren, 1955
P. liomedon	Ori.	Wynter-Blyth, 1957
P. machaon	Pal.	Seitz, 1909; Longstaff, 1912:46; deRhe-Philipe, 1932; Muspratt, 1954; Wynter-Blyth, 1957
P. m. aliaska	Nea.	Cary, 1907; Leussler, 1935; Rawson, 1955; Wyatt, 1957a
P. m. asiatica	Pal.	Hayward, 1937
P. m. centralis	Pal.	Peile, 1923
P. m. hippocrates	Pal.	Longstaff, 1912:46
P. macleayanus	Aus.	Waterhouse, 1932; new (Wyatt)
P. paris	Ori.	Wynter-Blyth, 1957
P. pelaus	Neo.	New (Turner)
P. podalirius	Pal.	Seitz, 1909; Muspratt, 1954
P. polymetus	Neo.	new (Kesselring)
P. polyxenes asterius	Nea.	Weed, 1901; Weiss, 1927; Clark, 1932; Merritt, 1952; Knudsen, 1954; Tilden, 1964
P. rex	Eth.	Van Someren, 1955
P. rudkini	Nea.	new (many)
P. rutulus	Nea.	new (Guppy, Scott, Tilden)
P. thersites	Neo.	Avinoff and Shoumatoff, 1946; Shoumatoff, 1953; new (Turner)
P. thoas	Neo.	new (Brown)
P. torquatus	Neo.	new (Brown)
P. troilus	Nea.	Weiss, 1927, 1928
P. zelicaon	Nea.	Mead, 1878; Osten-Sacken, 1882; Edwards, 1887; Snyder, 1894; Wright, 1906; Newcomer, 1910; Grinnell, 1915; Whitehouse, 1918; Van Dyke, 1919; Comstock, 1927; Garth, 1935; Merritt, 1952; Guppy, 1953; Emmel and Emmel, 1962; Garth and Tilden, 1963; Tilden, 1964
Papilio zelicaon-polyxenes hybrid (nitra)	Nea.	new (Scott)

TABLE 2 (continued)

Species	Realm	Sources
Teinopalpus imperialis	Ori.	Seitz, 1927; Parsons, 1948; Bailey, 1951; Saunders, 1955; Wynter-Blyth, 1957
Zetides cloanthus	Ori.	Bailey, 1951; Wynter-Blyth, 1957
PIERIDAE		
Coliadinae		
Eurema hecabe	Pal. Ori.	Longstaff, 1912:46, 388
Phoebis spp.	Neo.	new (Kesselring)
Pierinae		
Anthocaris belia	Pal.	Gurney, 1907
A. cethura	Nea.	Morrison, 1883; Comstock, 1927; Garth, 1934
A. falloui	Pal.	Fountaine, 1906
A. midea	Nea.	Rawson, 1951; Arnhold, 1952; Merritt, 1952; Shoumatoff, 1953; Knudsen, 1954
A. pima	Nea.	Beutenmuller, 1898; Wright, 1906; Comstock, 1927
A. tagis	Pal.	Gurney, 1907
Colotis bowkeri	Eth.	Trimen, 1889
C. eris	Eth.	Trimen, 1889
Daptonoura spp.	Neo.	new (Kesselring)
Delias harpalyce	Aus.	new (Wyatt)
D. nysa	Aus.	new (Wyatt)
Euchloe ausonides coloradensis	Nea.	Garth, 1934, 1935; Garth and Tilden, 1963
E. belemia	Pal.	Longstaff, 1912:162; Peile, 1923
E. belledice	Pal.	Longstaff, 1912:162
E. charlonia	Pal.	Longstaff, 1912:162; Dover, 1922; Wynter-Blyth, 1957
E. c. transcaspica	Pal.	Peile, 1923
E. hyantis	Nea.	Garth, 1934, 1935; Garth and Tilden, 1963
E. h. lotta	Nea.	Garth, 1934, 1935
E. olympia	Nea.	Clark and Clark, 1951; Arnhold, 1952; Merritt, 1952
E. o. rosa	Nea.	new (Justice)
Piercolias huanaco	Neo.	Seitz, 1924
Pieris callidice	Pal.	Muspratt, 1954
P. daplidice	Pal.	Longstaff, 1912:33
P. occidentalis	Nea.	Snyder, 1894; Dod, 1908a; Shepard, 1966
P. o. calyce	Nea.	new (many)

TABLE 2 (continued)

Species	Realm	Sources
Pieris protodice	Nea.	new (many)
P. rapae	Nea., Aus.	Scudder, 1887, 1889; Meinecke, 1917; Bryan, 1926
P. sisymbrii	Nea.	Tilden, 1964; new (many)
NYMPHALIDAE		
Danainae		
Ceratinia vallonia	Neo.	new (Kesselring)
Chittira fumata	Ori.	Longstaff, 1912:388
Euploea diocletiana	Ori.	Rawlins, 1949
Ideopsis gaura parakana	Ori.	Rawlins, 1949
Mechanitis nessaea	Neo.	new (Kesselring)
Thyridia singularis	Neo.	new (Kesselring)
Satyrinae		
Neominois ridingsii	Nea.	Comstock, 1927
Oeneis chryxus	Nea.	Snyder, 1894, 1897; McDunnough, 1927
O. c. ivallda	Nea.	Wright, 1906; Grinnell, 1915; Comstock, 1927; Martin and Ingham, 1930; Tilden, 1959; Garth and Tilden, 1963; Brown, 1965
O. c. stanislaus	Nea.	new (many)
O. marcounii	Nea.	Elwes and Edwards, 1893; Masters et al., 1967
O. melissa assimilis	Nea.	Freemen, 1948; Munroe 1951
O. m. beanii	Nea.	Elwes and Edwards, 1893; Dod, 1901, 1908a, 1908b; Fletcher, 1905; Nicholl, 1906; Fletcher and Gibson, 1908; Whitehouse, 1918; McDunnough, 1927
O. m. lucilla	Nea.	Mead, 1875; new (many)
O. nevadensis	Nea.	Edwards, 1887; Danby, 1894; Fletcher, 1906; Wright, 1906; Guppy, 1962
O. n. iduna	Nea.	Edwards, 1884
O. polixenes brucei	Nea.	Klots, 1937
Pararge hindukushica	Pal.	new (Wyatt)
P. megaera	Pal.	Fountaine, 1906; Peile, 1923; Scott, 1926; Temple, 1953; Muspratt, 1954
P. menava	Pal.	new (Wyatt)

TABLE 2 (continued)

Species	Realm	Sources
Pararge moera	Pal.	new (Wyatt)
Pharneuptychia spp.	Neo.	new (Brown)
Morphinae		
Brassolis spp.	Neo.	new (Brown)
Caligo spp.	Neo.	new (Brown)
Catoblepia spp.	Neo.	new (Brown)
Dasyophthalma spp.	Neo.	new (Brown)
Dynastor darius	Neo.	new (Brown)
Eryphanis spp.	Neo.	new (Brown)
Narope spp.	Neo.	new (Brown)
Opsiphanes spp.	Neo.	new (Brown)
Charaxinae		
Agrias spp.	Neo.	new (Brown)
Anaea, most species	Neo.	new (Brown)
A. ryphae	Neo.	new (Kesselring)
Charaxes achaemenes	Eth.	Van Someren, 1955
C. castor	Eth.	Van Someren, 1955
C. epijasius	Eth.	Van Someren, 1955
C. fabius	Ori.	Best, 1953, 1954
C. polyena imna	Ori.	Best, 1953, 1954
C. viola	Eth.	Van Someren, 1955
Eriboea athamas	Ori.	Best, 1953, 1954
E. pyrrhus sempronius	Aus.	new (Wyatt)
Euxanthe spp.	Eth.	Van Someren, 1955
Hamamumida daedulus	Eth.	Trimen, 1887; Van Someren, 1955
Prepona, most species	Neo.	new (Brown)
P. demophon	Neo.	new (Kesselring)
Siderone nemesis	Neo.	new (Kesselring)
Zäretes isidora	Neo.	new (Kesselring)
Nymphalinae		
Adelpha, many spec.	Neo.	new (Brown)
Ageronia februa	Neo.	new (Kesselring)
A. feronia	Neo.	new (Kesselring)
Argynnis hyperbius	Pal., Ori.	Longstaff, 1912:100; Fraser, 1916; Wynter-Blyth, 1957
A. lathonia	Pal.	Wynter-Blyth, 1957
A. l. issaea	Pal.	Longstaff, 1912:46, 64; Seitz, 1927
Boloria alberta	Nea.	Dod, 1901, 1908b; Nicholl, 1906; Wyatt, 1957b
B. astarte	Nea.	Dod, 1901, 1908a; Fletcher, 1905; Nicholl, 1906; Skinner, 1908; Whitehouse, 1918; Wyatt, 1957b

TABLE 2 (continued)

Species	Realm	Sources
Boloria polaris gronlandica	Nea.	Munroe, 1951
B. selene myrina	Nea.	Scudder, 1887, 1889
B. toddi	Nea.	Scudder, 1887, 1889
Chlosyne californica	Nea.	new (many)
C. ismeria	Nea.	Knudsen, 1954
C. i. carlota	Nea.	new (Justice, Scott)
C. leanira wrightii	Nea.	new (Breedlove)
C. theona	Nea.	new (Shields)
Doxocopa agathina	Neo.	new (Brown)
D. kallima	Neo.	new (Brown)
D. vacuna	Neo.	new (Brown)
D. zunilda	Neo.	new (Brown)
Dynamine mylitta	Neo.	new (Brown)
D. argyrippa	Neo.	new (Brown)
Eueides isabella	Neo.	new (Brown)
Euphydryas anicia	Nea.	Whitehouse, 1918
E. a. alena	Nea.	new (Scott)
E. a. brucei	Nea.	new (Justice)
E. a. capella	Nea.	new (Scott)
E. a. eurytion	Nea.	new (Scott)
E. chalcedona	Nea.	new (many)
E. c. sierra	Nea.	Brown, 1965
E. editha	Nea.	new (Scott, Thorne)
E. e. nubigena	Nea.	new (many)
Euripus consimilis	Ori.	Wynter-Blyth, 1957
Hestina nama	Ori.	Bailey, 1951
Historis spp.	Neo.	new (Brown)
H. odius	Neo.	Avinoff and Shoumatoff, 1946
H. orion	Neo.	new (Kesselring)
Limenitis archippus	Nea.	Scudder, 1887, 1889
L. arthemis	Nea.	Scudder, 1887, 1889
L. astyanax	Nea.	Weiss, 1927
L. lorquini	Nea.	Martin and Ingham, 1930
Melitaea didyma	Pal.	Peile, 1923
M. trivia	Pal.	Peile, 1923
M. t. persea	Pal.	Peile, 1923
Myscelia sophronia	Neo.	new (Brown)
M. orsis	Neo.	new (Brown)
Nymphalis antiopa	Nea.	Scudder, 1887, 1889 Weiss, 1927
N. californica	Nea.	new (Breedlove, Dvorak)
N. cashmiriensis	Pal.	Longstaff, 1912:46
N. milberti	Nea.	Scudder, 1863, 1887, 1889; Weed, 1901; Weiss, 1927; Garth, 1935; Garth and Tilden, 1963
N. urticae	Pal.	Muspratt, 1954
N. vau-album j-album	Nea.	Scudder, 1887, 1889; Weiss, 1927

TABLE 2 (continued)

Species	Realm	Sources
Phyciodes tharos	Nea.	Scudder, 1887, 1889
Poladryas pola	Nea.	new (Scott, Shields)
P. p. arachne	Nea.	new (Scott)
Polygonia egea	Pal.	Wynter-Blyth, 1957
P. faunus	Nea.	Scudder, 1863, 1874, 1887, 1889
P. gracilis	Nea.	Scudder, 1887, 1889
P. interrogationis	Nea.	Morrison, 1874; Scudder, 1887, 1889
Precis, 3 species	Eth.	Van Someren, 1955
P. orithyia	Pal.	Longstaff, 1912:46
Speyeria atlantis	Nea.	Scudder, 1887, 1889
S. callippe comstocki	Nea.	new (many)
S. c. meadii	Nea.	new (Scott)
S. c. nevadensis	Nea.	new (Shields)
S. coronis halcyone	Nea.	new (Scott)
S. edwardsii	Nea.	new (Scott)
S. egleis linda	Nea.	new (Ellis)
S. e. tehachapina	Nea.	Comstock, 1927; Emmel and Emmel. 1963a
S. hydaspe	Nea.	Shepard, 1966
S. mormonia	Nea.	Shepard, 1966
S. zerene bremnerii	Nea.	Edwards, 1887
S. z. platina	Nea.	new (Ellis)
Vanessa atalanta	Nea., Neo., Pal.	Mead, 1892; Dison, 1922; Moffat, 1922; Martin and Ingham, 1930; Shoumatoff, 1953; Muspratt, 1954; Emmel and Emmel, 1962
V. cardui	Nea. Pal., Eth., Ori., Aus.	Edwards, 1884; Longstaff, 1912:98, 162, 201, 385, 433; Dixon, 1922; Moffat. 1922; Seitz, 1924; Bryan, 1926; Weiss, 1927; Martin and Ingham, 1930; Tinkham, 1944; Tilden, 1961; Emmel and Emmel, 1962; Moucha, 1963
V. c. kershawi	Aus.	Longstaff, 1912:453
V. caryae	Nea.	Edwards, 1884; new (many)
V. dejeani	Ori.	Seitz, 1927
V. gonerilla	Aus.	Hudson, 1898; Longstaff, 1912:482
V. indica	Ori.	Longstaff, 1912:385
V. itea	Aus.	Hudson, 1898; Longstaff, 1912: 448
V. myrinna	Neo.	new (Brown)
V. tameamea	Aus.	Zimmerman, 1958

TABLE 2 (continued)

Species	Realm	Sources
Vanessa virginiensis	Nea.	Mead, 1892; Wright, 1908, 1930; Weiss, 1928; Martin and Ingham, 1930; Richards, 1931; Clark, 1932; Shoumatoff, 1953; Emmel and Emmel, 1962
V. v. brasiliensis	Neo.	new (Brown)
Acraeinae		
Acraea ssp.	Eth.	Van Someren, 1955
Actinote, most spec.	Neo.	new (Brown)
LYCAENIDAE		
Riodininae		
many species, nearly 40 on one hilltop in Rio de Janeiro	Neo.	new (Brown)
Dodona ouida	Pal.	Wynter-Blyth, 1957
Nymula calyce	Neo.	new (Brown)
Lycaeninae		
Aphnaeus spp.	Eth.	Van Someren, 1955
Arcas, many species	Neo.	new (Brown)
Argiolaus spp.	Eth.	Van Someren, 1955
Atlides, many species	Neo.	new (Brown)
A. halesus	Nea.	new (many)
Callophrys dumetorum	Nea.	new (Shields, Thorne)
C. viridis	Nea.	new (Gorelick)
Celastrina argiolus echo	Nea.	new (Shields)
C. a. ladonidas	Pal.	Longstaff, 1912:142
C. a. pseudargiolus	Nea.	Scudder, 1887, 1889
C. lanka	Ori	Longstaff, 1912:388
C. puspa	Ori.	Wynter-Blyth, 1957
C. singalensis	Pal.	Longstaff, 1912:46
Egumbia spp.	Eth.	Van Someren, 1955
Epamera spp.	Eth.	Van Someren, 1955
Evenus, many species	Neo.	new (Brown)
Everes argiades	Pal.	Muspratt, 1954
E. comyntas	Nea.	Weiss, 1928
E. diporides	Pal.	Wynter-Blyth, 1957
Incisalia eryphon	Nea.	new (Dvorak)
I. fotis	Nea.	new (Henne, Shields)
I. iroides	Nea.	new (Thorne)
I. iroides-fotis (hybrid)	Nea.	new (Henne)
I. niphon	Nea.	Scudder, 1889
Lampides boeticus	Aus.	Bryan, 1926
Lepidochrysops spp.	Eth.	Van Someren, 1955
Leptotes marina	Nea.	new (Shields)
Lycaena sallustius	Aus.	Longstaff, 1912:482

TABLE 2 (continued)

Species	Realm	Sources
Miletis delicia	Aus.	new (Wyatt)
Mitoura spinetorum	Nea.	Shields, 1965
Myrina spp.	Eth.	Van Someren, 1955
Ogyris genoveva	Aus.	new (Wyatt)
Polyommatus baeticus	Pal., Ori.	Longstaff, 1912:64, 388
Pratapa blanka	Ori.	Wynter-Blyth, 1957
Pseudodipsas brisbanesis	Aus.	new (Wyatt)
Satyrium behrii	Nea.	new (Emmel, Scott, Shields)
S. calanus	Nea.	Weiss, 1927
S. saepium	Nea.	new (Emmel, Shields)
S. titus	Nea.	new (Shields)
Spindasis spp.	Eth.	Van Someren, 1955
Strymon columella	Nea.	new (Shields)
S. melinus	Nea.	Tilden, 1964; new (many)
Tajuria spp.	Ori.	Wynter-Blyth, 1957
Talicada nyseus	Ori.	Longstaff, 1912:98
Thecla spp.	Ori.	Wynter-Blyth, 1957
Theclini, a great number of species	Neo.	new (Brown)
Virachola spp.	Eth.	Van Someren, 1955
V. isocrates	Ori.	Wynter-Blyth, 1957
HESPERIIDAE		
Coeliadinae		
Bibasis sena	Ori.	Longstaff, 1912:357; Wynter-Blyth, 1957
Coeliades forestans	Eth.	Van Someren, 1955
Pyrrhopyginae		
many species	Neo.	new (Brown)
Trapezitinae		
"The majority" of 51 species in Australia	Aus.	Waterhouse, 1932
Hesperilla idothea	Aus.	new (Wyatt)
Toxidia peroni	Aus.	new (Wyatt)
Trapezites iacchoides	Aus.	new (Wyatt)
T. iacchus	Aus.	new (Wyatt)
T. phigalia	Aus.	new (Wyatt)
Pyrginae		
many crepuscular species	Neo.	new (Brown)
Astraptes spp.	Neo.	new (Brown)
Baracus vittatus	Ori.	Longstaff, 1912:388
Celaenorrhinus ambareesa	Ori.	Longstaff, 1912:391
Epargyreus spp.	Neo.	new (Brown)
Erynnis afranius	Nea.	Snyder, 1894 (as lucilius); Emmel and Emmel, 1962
E. brizo	Nea.	new (Scott)

TABLE 2 (continued)

Species	Realm	Sources
Erynnis brizo burgessi	Nea.	Freeman, 1951
E. b. lacustra	Nea.	new (many)
E. horatius	Nea.	new (Scott)
E. icelus	Nea.	Scudder, 1887, 1889; Tilden, 1964; new (Scott)
E. martialis	Nea.	new (Scott)
E. meridianus	Nea.	Freeman, 1951
E. pacuvius	Nea.	Grinnell, 1904; new (Shields)
E. p. callidus	Nea.	Grinnell, 1904; new (Shields)
E. p. pernigra	Nea.	new (La Due, MacNeill)
E. persius fredericki	Nea.	new (Scott, Shields)
E. propertius	Nea.	new (Shields)
E. telemachus	Nea.	new (Scott)
E. tristis	Nea.	Freeman, 1951; new (Shields)
Phocides spp.	Neo.	new (Brown)
Sarangesa dasahara	Ori.	Longstaff, 1912:391
S. purendra	Ori.	Longstaff, 1912:391
Thorybes bathyllus	Nea.	Weiss, 1927; Clark, 1936a
T. confusis	Nea.	Clark, 1936a
T. mexicana nevada	Nea.	new (many)
T. pylades	Nea.	Weiss, 1927; Clark, 1936a
Urbanus spp.	Neo.	new (Brown)
Zestusa dorus	Nea.	new (Scott, Shields)
Hesperiinae		
Abantis paradisea	Eth.	Van Someren, 1955
A. tettensis	Eth.	Van Someren, 1955
Amblyscirtes vialis	Nea.	Weiss, 1927
Hesperia columbia	Nea.	new (Shields, Tilden)
H. comma	Nea.	new (Grey)
H. harpalus ochracea	Nea.	new (Scott)
H. harpalus yosemite	Nea.	new (Shields)
H. juba	Nea.	new (Roever, Scott)
H. leonardus	Nea.	new (Grey)
H. metea	Nea.	Clench, 1966
H. miriamae	Nea.	Garth and Tilden, 1963 new (Shields)
H. nevada	Nea.	new (many)
H. pahaska	Nea.	new (Scott)
H. p. martini	Nea.	new (MacNeill, Scott)
H. p. williamsi	Nea.	new (Shields)
H. pawnee	Nea.	new (Scott)
H. sassacus	Nea.	new (Grey)
H. uncas	Nea.	new (Scott, Shields)
H. u. macswaini	Nea.	new (MacNeill)
H. viridis	Nea.	new (Scott, Shields)

TABLE 2 (continued)

Species	Realm	Sources
Polites sonora	Nea.	new (MacNeill)
P. themistocles	Nea.	Scudder, 1887, 1889
Stinga morrisoni	Nea.	Tilden, 1961 new (Scott, Toliver)

Nea. = Nearctic
Neo. = Neotropical
Pal. = Palearctic
Eth. = Ethopian
Ori. = Oriental
Aus. = Australian

Note: many of these species are listed from various sources which mentioned in passing that a species frequented topographic prominences. Some of these may not represent hilltopping species and therfore further work to confirm or deny their validity is needed, in light of the mating-rendezvous definition of hilltopping.

eight mating pairs of Diptera on Squaw Peak, Montana. Edwards (1960) noted mating activities in summit tachinid and syrphid flies. A more detailed analysis of this mating theory will appear in the discussion section.

"Swarms" of male insects are associated with mating and are sometimes present on summits. Although Craig (1944) and Nielsen and Greve (1950) claim that certain Diptera swarms were not formed for mating, other workers have found that mating occurs when females enter male swarms in a variety of families (Knab, 1907; Gibson, 1942; Bailey, 1948; Downes, 1958; Blickle, 1959; Shemanchuk and Weintraub, 1961; Powell, 1964b; Thompson, 1967). Swarming of winged ants is also associated with mating (Wheeler, 1917b; Michener, 1948, 1960; Chapman, 1954b, 1957, 1963). In the biting Nematocera flies, the swarm develops visually to a "swarm-marker" such as a clearing or summit where both sexes respond to the marker; such swarms function to concentrate the population for the purpose of mating (Downes, 1958).

Another theory often given to explain the presence of insects on summits is that wind bears them up, particularly warm air updrafts. This idea has been mentioned for insects in general by Bowditch (1896), Guppy (1897), Rowland-Brown (in Poulton, 1904), Meinecke (1917), Bryan (1926), and Alexander (1940), and for winged ants by Wheeler (1905, 1917a) and Gregg (1947). As Chapman (1954a, 1954b, 1957) pointed out, however, updrafts may account for the presence of some but not all insects on summits (see Discussion).

Current theories to explain "hilltopping" in butterflies are reviewed by Shoumatoff (1953) and Shepard (1966). Apparently, Shepard (1966) is the only person to have made observations of more than a casual nature on hilltopping butterflies by using a mark-recapture technique. It appears that little attempt has been made in the past to apply to butterflies the findings for other summit-frequenting insects.

The different theories for the "hilltopping" of butterflies are listed in Table 3. Wind theories can be dispelled for the same reasons mentioned by Chapman (1954a) for insects (see Discussion). The presence of larval foodplants on summits can be ruled out as a theory since many hilltopping species ascend far away from the foodplant area (see, for example, Clark, 1936a; Muspratt, 1954; Emmel & Emmel, 1967) as pointed out by Knudsen (1954) and Van Someren (1955). Males "liking" hilltops as a playground, battleground, or assembly area or as a

TABLE 3. Butterfly hilltopping theories

Theory	Sources
1. Wind and/or updraft transported	Newcomer, 1910 Guppy, 1925 Merritt, 1952 Beall, 1953 Knudsen, 1954 Rawson, 1955 Shepard, 1966
2. Wind on summit as enticement	Beutenmuller, 1898 Muspratt, 1954 Emmel and Emmel, 1962
3. Unidirectional flight plus wind	Beall, 1953 Shepard, 1966
4. "Liking" hilltops (urge to ascend)	Scudder, 1863:620 Wright, 1906:86 Merritt, 1952 Shoumatoff, 1953
5. Ascend for "assemblying"	Beutenmuller, 1898
6. Male surplus	Merritt, 1952
7. Male "playground" or "sporting ground"	Comstock, 1927:20, 42, 265 Clark, 1932:192 Clark, 1936a:24-25 Clark, 1936b:384, 405 Barrett and Burns, 1951:4-5, 144
8. Male "battleground"	Wright, 1906:86. 112 Rawson, 1951
9. Tropism	Merritt, 1952
10. "Phototropic urge" (attraction to warmth and light)	Van Someren, 1955
11. Foodplant on summit	Wright, 1906:112 Arnhold, 1952 Merritt, 1952 Emmel and Emmel, 1962
12. Congregation point for mating	Seitz, 1909:13, 14 Moffat, 1922 Peile, 1923:62 Clark, 1932:192 Guppy, 1962 Emmel and Emmel, 1967

response to a tropism urge does not go far in explaining the phenomenon because natural selection would eradicate this tendency for males to congregate away from females (Guppy, 1962). Surplus males congregating on summits due to the "extrovertive" male flight behavior is probably a misconception (Shepard, 1966). The idea that updrafts congregate butterflies due to the hilltop interrupting the butterfly's undirectional flight (Shepard, 1966) is inadequate because the event occurs also on still days (Knudsen, 1954) and because of the "up-and-over" tendency observed for nonhilltopping species reported here. The ideas that hilltops are meeting areas for the sexes to mate, shown to be the explanation for certain other insects, will be presented and discussed in detail in this paper as the best explanation of the phenomenon of hilltopping in butterflies.

MATERIALS AND METHODS

Observations were made continuously from March 1966 to April 1968 (except for the months of July and August), with emphasis on the winter and spring months. A total of 245 hours on 170 days was spent observing and collecting on the summit of Dictionary Hill, San Diego County, California. Some observations were made for an entire day, but most were for one to four hours, generally between midmorning and midafternoon.

Visual sightings of species in the field were recorded. Activities such as perching, feeding, chasing, courtship, mating, roosting, and predation were noted as they occurred. The occurrence and behavior of females on the summit were particularly checked to determine the validity of the summit-mating theory. Careful note was made of all species present on the summit and whether they exhibited hilltopping behavior or "up-and-over" flight. The proximity of larval foodplants of these species to the summit was checked. Flight behavior in relation to wind and updrafts was noted.

Butterflies were collected with an insect net in the air or when they alighted. All identifications were made to species. Extensive marking of male hilltopping butterflies was done to determine the habits of individuals of each species. A total of 1,011 specimens was marked. The "1-2-4-7" system (Ehrlich & Davidson, 1960) was soon found to be the best method for marking and satisfied most of the criteria for an ideal marking technique described by Gangwere et al. (1964). Eight different colored "Marks-A-Lot" felt-tip pens were used. The dye stain left on the wing was quick-drying, waterproof, and permanent without

affecting flight. Specimens could be marked quickly and recognized individually by this method. The maximum number that could be marked at one time with one color was 154. Papilionidae and Nymphalidae were held gently with wings shut between thumb and forefinger for application of the marks to the wing underside. The more delicate Pieridae, Lycaenidae, and Hesperiidae were marked through the netting after being gently confined. Marked specimens were not placed in glassine envelopes except in release experiments. In most cases butterflies had to be recaptured for their numbers to be read.

Marking had no apparent injurious effect on the individual. Released specimens either alighted, flew rapidly downhill, or resumed their previous activity. Many specimens marked that initially flew downhill soon returned. "Normal" activities were seen to resume in many marked specimens. For example, often two males that were chasing each other when netted continued doing so when released. Also, males frequently returned to perch in a previous territory or "fly" area after marking. Specimens were not always released at the point of capture but were always released on the summit immediately after marking. Number, sex, wing condition, and time of capture were recorded for each marked specimen.

The *Papilio zelicaon* males used in release experiments away from the hill were netted, marked, placed in glassine envelopes, and stored in a cigar box which was kept in the shade. These experiments were carried out during periods when their population density was low so that their recapture was easier. *P. zelicaon* was used because its presence was conspicuous and it was relatively easy to recapture.

Females were collected on the summit whenever possible to check if they were mated or virgin. Male Lepidoptera deposit sperm in membranous saclike spermatophores. The bursa copulatrix of each female was later dissected under a binocular dissecting scope to check for the presence of a spermatophore (see Ouye et al., 1964; Burns, 1966; Taylor, 1967). Also, bursae from females of certain species from nonhilltop areas were dissected for comparison. A total of 548 bursae was examined during the survey: 281 from hilltop areas and 267 from nonhilltop areas. The two assumptions that Burns (1966) made are also assumed here: (1) the male transfers one spermatophore per mating, and (2) the spermatophore walls can be recognized even when collapsed. Females lacking a spermatophore were assumed to be virgin; such females were usually in fresh wing condition.

Collected females were either stored under refrigeration or their abdomens were transferred to 80 percent ethyl alcohol for later inspection. Dried females were checked from previous collections. Their abdominal tissues were reclaimed for dissection by the technique described by Van Cleve and Ross (1947), which consists of soaking the abdomens for 24 to 72 hours in a solution of trisodium phosphate diluted to 0.5 percent with distilled water.

Weather readings were taken when *in copula* pairs were observed and at the time that hilltoppers first arrived for the day. Air temperature, relative humidity, and wind velocity were recorded on the summit by taking head-high readings with a Dwyer anemometer and a Bacharach sling psychrometer. Pacific Standard Time was used throughout the study.

For comparative purposes, certain other summits in San Diego County were occasionally visited to mark and observe hilltopping species. These included a hill 997 feet in elevation, 1.7 miles south-southeast of the El Cajon Post Office; a hill 842 feet high 0.9 miles east of Dictionary Hill; Cowles Mountain; Tecate Mountain; Monument Peak; Mount Kentwood; and "Two Mile Hill," one mile west of Scissors Crossing, 6.5 air miles east of Julian.

Location and Description of Study Area

Dictionary Hill is 1,064 feet in elevation and is located one mile south of Spring Valley and 1.75 mile north of Sweetwater Reservoir (T. 17 S., R. 1 W., Sects. 5, 32, 33), San Diego County, California (Fig. 1). The nearest higher hills are Mount Helix (1,373 feet), 2.9 air miles to the north-northeast; Mother Miguel Mountain (1,527 feet), 3.3 air miles to the south-southeast; and San Miguel Mountain (2,565 feet), 3.9 air miles to the southeast. Three lesser knobs on the eastern slopes of Dictionary Hill are 924 feet, 842 feet, and 677 feet high. The surrounding lowlands range from 200 to 800 feet below the summit of the hill.

The hill consists of Jurassic-Triassic meta-volcanic rocks, with a rough stony land soil-type. The climate of the area is dry summer Mediterranean. La Mesa, California, at 560 feet, located three miles to the north of Dictionary Hill, has the following climatic features: the average maximum temperature is 75.0° F, the average minimum temperature is 50.0° F, the average mean temperature is 62.5° F, the average number of days with 0.01 inches or more precipitation is 44, and the average growing season is 327 days (Felton, 1965).

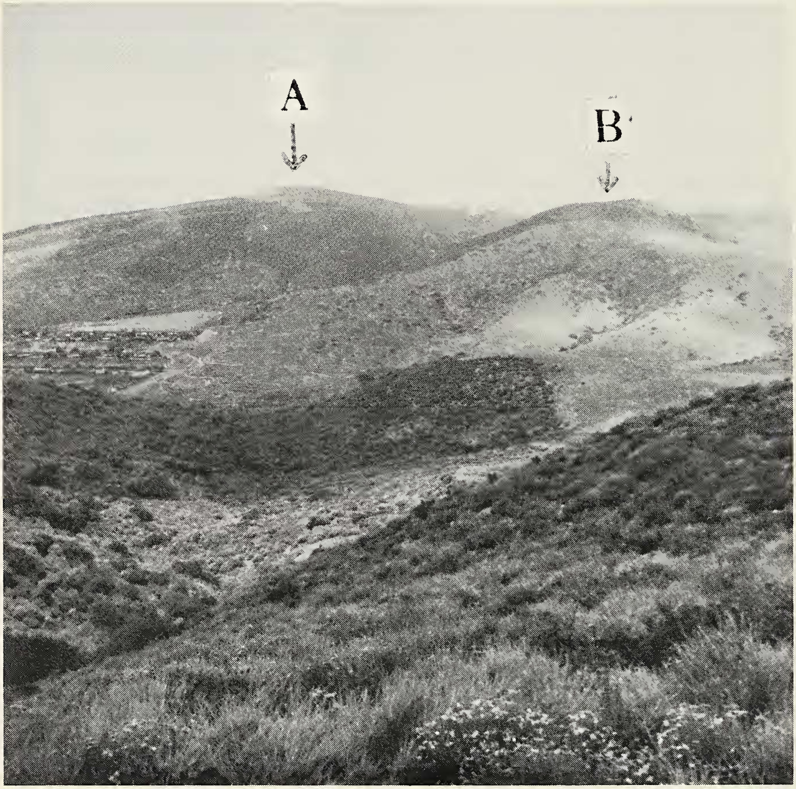

Fig. 1. Dictionary Hill (A) and Hill 842 (B), as seen from the southeast.

The plant community on the slopes of Dictionary Hill is Coastal Sage Scrub, according to the classification of Munz and Keck (1965). Indicator plants present include California Sagebrush (*Artemisia californica*), California Buckwheat (*Eriogonum fasciculatum*), Golden Yarrow (*Eriophyllum confertiflorum*), White Sage (*Salvia apiana*), and Black Sage (*S. mellifera*). Four conspicuous shrubs present are Broom Baccharis (*Baccharis sarothroides*), Monkey-flower (*Mimulus puniceus*), Redberry (*Rhamnus crocea*), and Laurel Sumac (*Rhus laurina*). Other plants on the slopes include Locoweed (*Astragalus* sp.), Slender Wild Oat (*Avena barbata*), Black Mustard (*Brassica nigra*), Blue Dicks (*Brodiaea pulchella*), White Forget-me-not (*Cryptantha intermedia*), Dodder (*Cuscuta* sp.), Tansy-Mustard (*Descurainia* sp.), Sweet Fennel (*Foeniculum vulgare*), certain grasses, Deerweed (*Lotus scoparius*), Plantain (*Plantago Hookeriana* var. *californica*), Figwort (*Scrophularia californica*), Wild Pansey (*Viola pedunculata*), and others.

The summit of Dictionary Hill was graded at one time and presents an elliptically shaped flat area measuring about 230 by 275 feet (Fig. 2). This area is covered by Broom Baccharis. Most of the observations were made near sumac clumps at the northeast and southwest edges, where hilltopping activity was most intense.

In the fall of 1958 a fire destroyed the vegetation on the western slope of Dictionary Hill. The area has since grown back considerably, but the fire probably destroyed a colony of *Chlosyne leanira wrightii,* a species that was common on the summit from 1955-1958. Three males were collected there on April 3, 1960, but none have been taken since that time. Its foodplant, *Castilleja* sp., grew on the west slope. *C. l. wrightii* specimens used to fly in areas where *Papilio zelicaon* and *Euphydryas chalcedona* hilltopped on the summit (Breedlove, personal communication). Thus *C. l. wrightii* may have been another hilltopping species.

RESULTS

Species Present

Forty-five species of butterflies were collected on the summit of Dictionary Hill during 1966-1968. A forty-sixth species, *Chlosyne leanira wrightii,* has not been collected there since 1960 (Table 4 and Fig. 3 and 4). Twenty-one of these were considered as hilltoppers because of their territorial or patrol behavior of males confined to the summit, as opposed to the twenty-five non-hilltopping species that flew "up-ond-over," fed without remaining, or did not congregate at the summit (Table

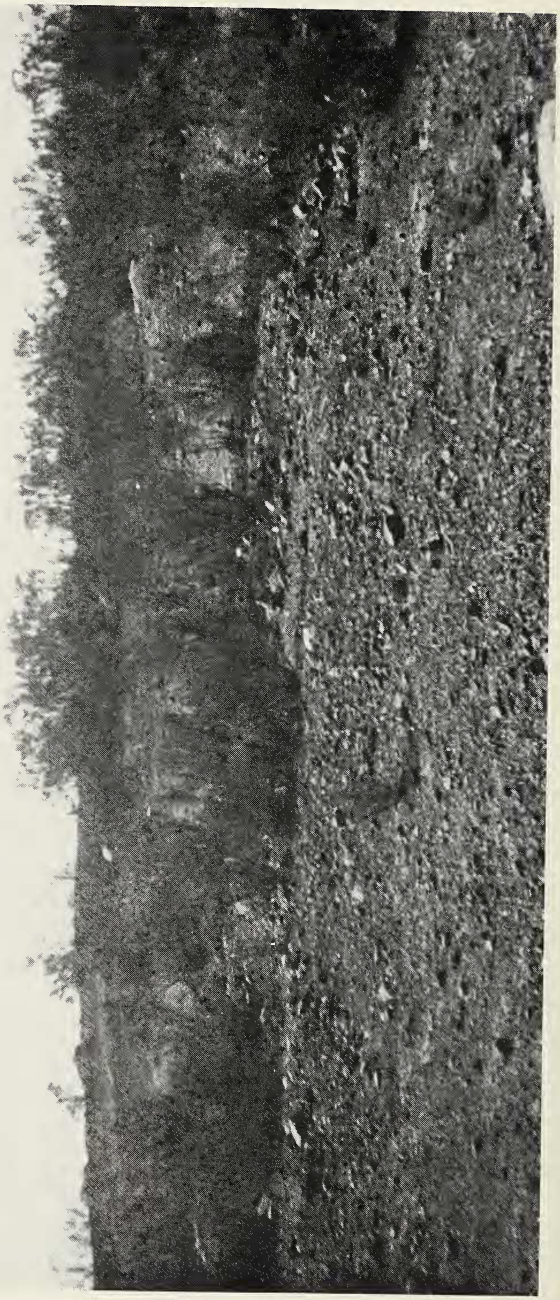

Fig. 2. Dictionary Hill summit with Broom Baccharis.

TABLE 4. Summit of Dictionary Hill, Spring Valley San Diego County, California. Species present collected by Oakley Shields

Hilltoppers	Non-hilltoppers
PAPILIONIDAE	PIERIDAE
Battus philenor	*Anthocaris sara*
Papilio eurymedon	*Colias eurytheme*
Papilio zelicaon	*Colias harfordii*
PIERIDAE	*Zerene cesonia*
Anthocaris cethura	*Eurema nicippe*
Pieris protodice	*Phoebis sennae*
NYMPHALIDAE	+ *Pieris rapae*
Chlosyne leanira wrightii	NYMPHALIDAE
Euphydryas editha	*Agraulis vanillae*
Euphydryas chalcedona	*Chlosyne gabbi*
Speyeria callippe comstocki	*Coenonympha tullia californica*
Vanessa atalanta	*Danaus plexippus*
Vanessa cardui	*Danaus gilippus berenice*
Vanessa caryae	*Junonia coenia*
Vanessa virginiensis	*Nymphalis antiopa*
LYCAENIDAE	LYCAENIDAE
Atlides halesus	* *Apodemia mormo virgulti*
Callophrys dumetorum	*Brephidium exilis*
Celastrina argiolus echo	+ *Everes comyntas*
Incisalia iroides	*Glaucopsyche lygdamus australis*
Leptotes marina	*Lycaena helloides*
Satyrium saepium	* *Philotes battoides bernardino*
Strymon melinus	HESPERIIDAE
HESPERIIDAE	*Erynnis funeralis*
Erynnis tristis	*Heliopetes ericetorum*
	Hylephila phyleus
	* *Ochlodes sylvanoides*
	Pyrgus communis

Total number of species = 46

0/0 of total that are hilltoppers = 45.7

+ = reported in the literature as hilltopping

* = species that rarely showed a territorial or aggressive activity but did not concentrate on the summit

5). Of these non-hilltopping species persent, both *Apodemia mormo virgulti* and *Everes comyntas* remained on and near the summit and one *in copula* pair was observed at the summit for both. However, these species were not particularly concentrated at the summit and occurred in about equal numbers on the slopes of Dictionary Hill as well. During 1960 K. Roever found 28 butterfly species on "A" Mountain summit, Tucson, Arizona (Table 6). The proportion of hilltopping species to non-hilltopping species at "A" Mountain and Dictionary Hill was remarkably similar (46% at both locations were hilltopping species).

Certain species were present in the canyon bottoms to the east, southeast, and south of Dictionary Hill (2,000-5,000 feet away from the summit) that were not collected on the summit: *Pieris beckerii, Philotes sonorensis, Poanes melane,* and *Urbanus proteus* (one). All but the last named were regular residents of the canyon bottoms, along with the non-hilltopping species *Anthocaris sara, Nymphalis antiopa, Junonia coenia,* and *Chlosyne gabbii* that were occasionally present on the summit.

Territorial and Aggressive Behavior

Most of the specimens that showed hilltopping behavior were males. This fact was determined by visual observation and capture of the 21 hilltopping species. In those species where the sexes were difficult to determine visually (e.g., *Vanessa* and *Erynnis*), captured specimens were nearly always males.

All of the hilltopping males except two pierid species established perch sites (*P. protodice* and *A. cethura* milled about without landing except occasionally to feed). The preferred perch site of *V. atalanta, V. cardui, V. carye,* and *C. dumetorum* was the ground or vegetation close to the ground. *V. atalanta* seemed especially partial to perching on rocks in clearings (Fig. 5). *V. virginiensis* was the only *Vanessa* species to consistently perch off the ground on vegetation (one to three feet up), although the others did so sometimes. Other species that perched on vegetation well above ground were *B. philenor, P. eurymedon, P. zelicaon* (Fig. 6) (on the ground occasionally), *A. halesus, S. melinus* (Fig. 7), *S. saepium, C. a. echo,* and *E. tristis* (Fig. 8). *E. chalcedona* perched on the ground, ground vegetation, and rocks in clearings and sometimes on vegetation one to two feet up. *B. philenor* and *P. eurymedon* rarely alighted and flew almost continuously in milling over the summit. Once landed, perched species usually faced perpendicular to the sun's rays.

The pattern of establishing and returning to perch sites was noted. *P. zelicaon* flew back and forth over an area and alighted

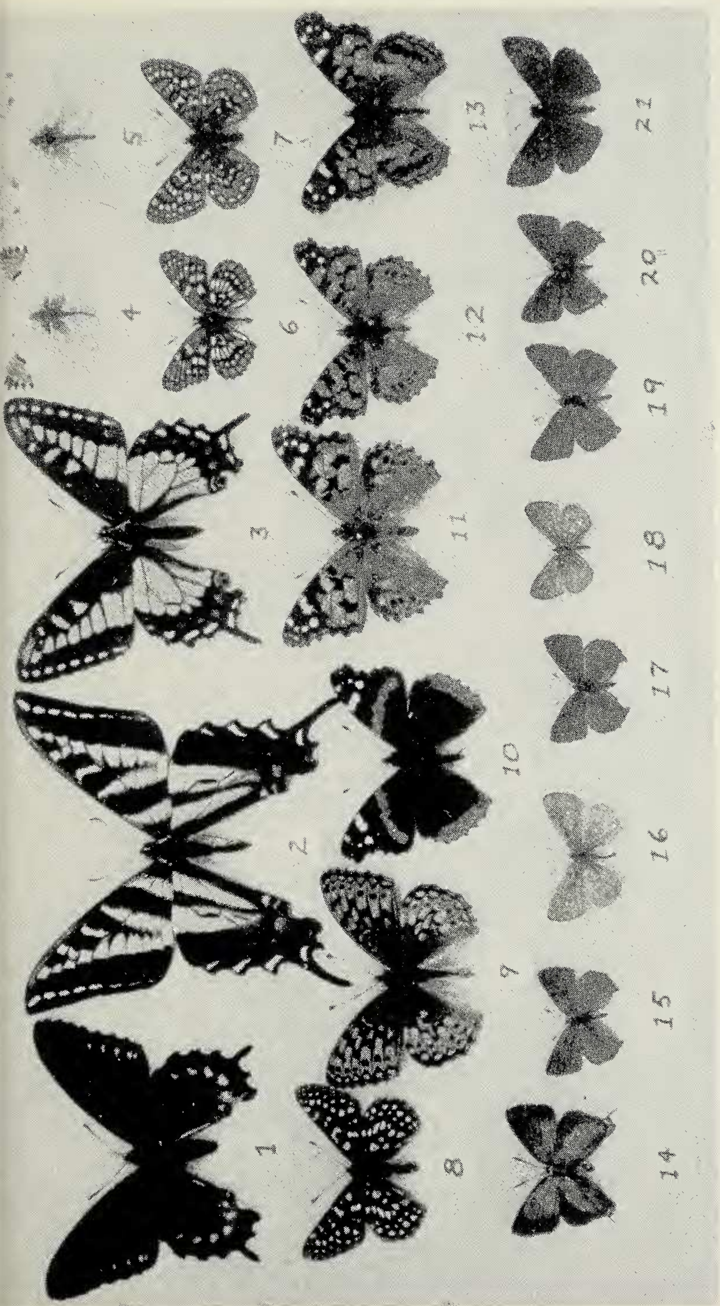

Fig. 3. Species of hilltopping butterflies from the summit of Dictionary Hill, males only: (1) *Battus philenor*, (2) *Papilio eurymedon*, (3) *Papilio zelicaon*, (4) *Anthocaris cethura*, (5) *Pieris protodice*, (6) *Chlosyne leanira wrightii*, (7) *Euphydryas editha*, (8) *Euphydryas chalcedona*, (9) *Speyeria callippe comstocki*, (10) *Vanessa atalanta*, (11) *Vanessa cardui*, (12) *Vanessa caryae*, (13) *Vanessa virginiensis*, (14) *Atlides halesus*, (15) *Callophrys dumetorum*, (16) *Celastrina argiolus echo*, (17) *Incisalia iroides*, (18) *Leptotes marina*, (19) *Satyrium saepium*, (20) *Strymon melinus*, (21) *Erynnis tristis*.

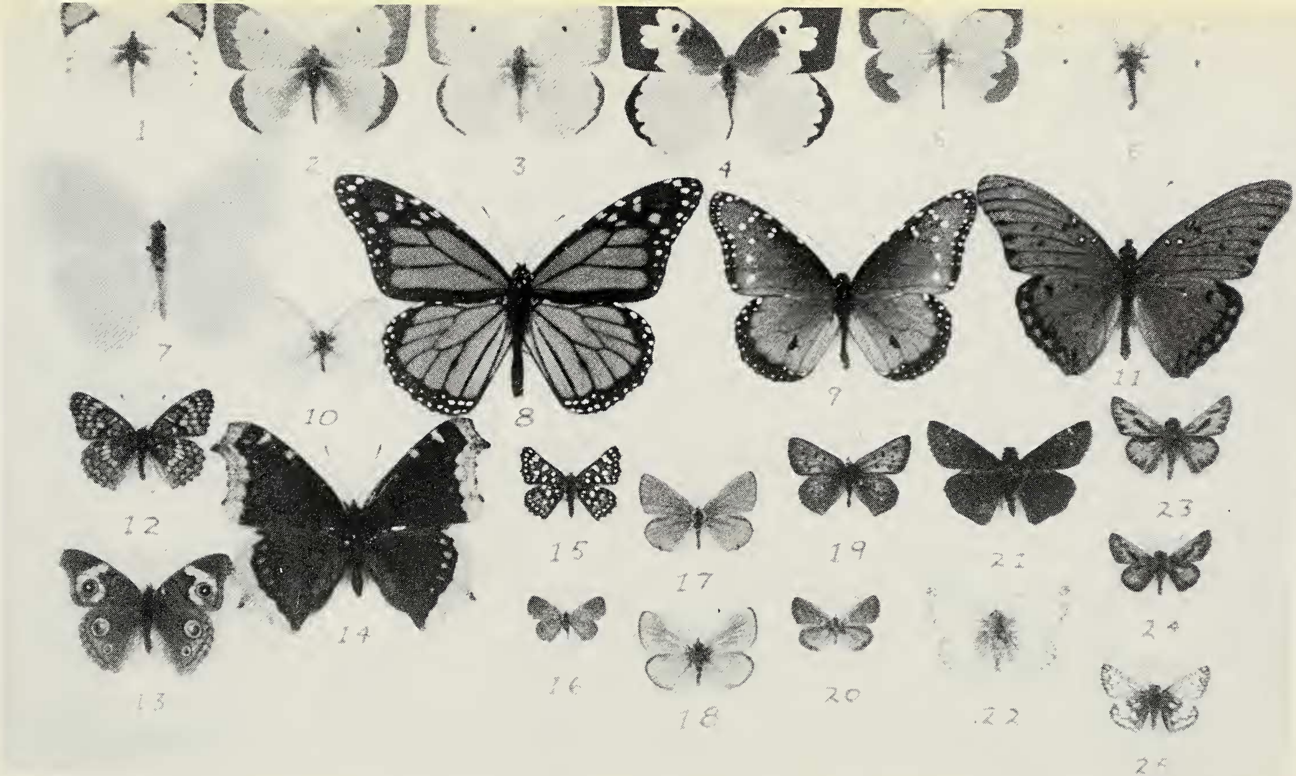

Fig. 4. Species of non-hilltopping butterflies from the summit of Dictionary Hill, males only: (1) *Anthocaris sara*, (2) *Colias eurytheme*, (3) *Colias harfordii*, (4) *Zerene cesonia*, (5) *Eurema nicippe*, (6) *Pieris rapae*, (7) *Phoebis sennae*, (8) *Danaus plexippus*, (9) *Danaus gilippus berenice*, (10) *Coenonympha tullia californica*, (11) *Agraulis vanillae*, (12) *Chlosyne gabbii*, (13) *Junonia coenia*, (14) *Nymphalis antiopa*, (15) *Apodemia mormo virgulti*, (16) *Brephidium exilis*, (17) *Everes comyntas*, (18) *Glaucopsyche lygdamus australis*, (19) *Lycaena helloides*, (20) *Philotes battoides bernardino*, (21) *Erynnis funeralis*, (22) *Heliopetes ericetorum*, (23) *Hylephila phyleus*, (24) *Ochlodes sylvanoides*, (25) *Pyrgus communis*.

TABLE 5. Non-hilltoppers present on the summit of Dictionary Hill during 1966-1968

Species	Comments
1. *Anthocaris sara*	Both sexes flying over, mostly females, occasional oviposition behavior.
2. *Colias eurytheme*	Both sexes flying over.
3. *Colias harfordii*	One male flying over.
4. *Zerene cesonia*	One male flying over.
5. *Eurema nicippe*	Some seen flying over, one female collected.
6. *Pieris rapae*	Both sexes flying and feeding.
7. *Phoebis sennae*	Two males flying over.
8. *Danaus gilippus berenice*	One male flying over.
9. *Danaus plexippus*	Several seen flying over.
10. *Coenonympha tullia californica*	A few males flying over.
11. *Agraulis vanillae*	Two males collected, other specimens seen flying over.
12. *Chlosyne gabbi*	Male and female collected.
13. *Junonia coenia*	A few seen flying over.
14. *Nymphalis antiopa*	A number seen flying over, Two males territorial.
15. *Apodemia mormo virgulti*	Both sexes present in numbers on summit but no concentrations; two *in copula* pairs collected *near* summit.
16. *Brephidium exilis*	Male and female feeding.
17. *Everes comyntas*	Males and females flying near summit, one *in copula* pair collected *near summit.*
18. *Glaucopsyche lygdamus australis*	Males flying over, females occasionally present.
19. *Lycaena helliodes*	A female feeding.
20. *Philotes battoides bernardino*	Two males territorial.
21. *Erynnis funeralis*	A number seen, several males and a female collected flying over and feeding.
22. *Heliopetes ericetorum*	Several males flying over, one male collected.
23. *Hylephila phyleus*	One male feeding.
24.+*Ochlodes sylvanoides*	Two males territorial.
25. *Pyrgus communis*	Occasional specimens flying over.

+ Not enough present to say if males preferred the summit or not.

TABLE 6. Summit of "A" Mountain, West of Tucson, Pima County, Arizona. Species present during 1960, collected by Kilian Roever

Hilltoppers	Non-hilltoppers
PAPILIONIDAE	PIERIDAE
Battus philenor	Anthocaris sara
Papilio polyxenes asterius	Colias eurytheme
Papilio rudkini	Eurema nicippe
	Nathalis iole
	Phoebis sennae
PIERIDAE	Zerene cesonia
Anthocaris pima	NYMPHALIDAE
Euchloe hyantis lotta	Agraulis vanillae
Pieris protodice	Asterocampa leilia
NYMPHALIDAE	Chlosyne lacinia
Vanessa atalanta	Danaus gilippus strigosus
Vanessa cardui	Danaus plexippus
Vanessa caryae	LIBYTHEIDAE
Vanessa virginiensis	Libytheana bachmanii
LYCAENIDAE	LYCAENIDAE
Atlides halesus	+ Leptotes marina
Strymon melinus	
HESPERIIDAE	HESPERIIDAE
Hesperia pahaska williamsi	Erynnis funeralis
	Pyrgus communis

Total number of species = 28
0/0 of total that are hilltoppers = 46.4
+ = reported in this paper as hilltopping.

Fig. 5. Male *Vanessa atalanta* in perched position.

Fig. 6. Male *Papilio zelicaon* in perched position.

Fig. 7. Male *Strymon melinus* in perched position.

Fig. 8. Male *Erynnis tristis* in perched position.

on plants within the same area after leaving the first perch in chases. Three *P. eurymedon* observed on different days flew lazily about the northeast side of the summit for about ten minutes before landing on the same sumac bush. *E. chalcedona* usually perched at various places in a particular clearing after each chase from a perch. All the *Vanessa* species seemed indifferent about where they would perch. They were not drawn to a particular spot or clearing and readily established a new perch area after a chase. All of the three *A. halesus* males perched on a particular sumac on the northeast top.

From these perch sites, investigative flights directed at the the same species, different species, and sometimes different insects were taken. When an individual of the same species passed a perched male, the perched male flew up to investigate, gave pursuit, and frequently engaged in a "battle" with the other male. Perched *P. zelicaon* males rapidly pursued passing *P. zelicaon* for considerable distances before breaking away and returning to the vicinity of the perch. Sometimes three or fuor *P. zelicaon* pursued in a chain. Frequently two *P. zelicaon* males would engage in a "battle," especially when males first established their territories during the morning. They flew in tight circles around each other and climbed high into the air, sometimes locking legs and audibly beating wings. (Eff [1962] has observed that *Papilio indra minori* males may physically damage each other in such encounters by beating their wings and falling to the ground while their legs are locked together.) *E. chalcedona*, *S. melinus*, and *C. dumetorum* were often seen to spin about each other in these high, climbing flights before breaking away and returning to the perch area. When two males of a *Vanessa* species met, they climbed at a slight angle to the ground, usually into the wind, with the pursuer behind the pursued. In all cases where identity could be determined by identifiable wing defects or marked specimens, it was the original male that returned after leaving the perch in the territorial species. This is what has been observed with territorial males in *Hesperia* (MacNeill, 1964), *Hesperia metea* (Shapiro, 1965), *Agathymus evansi* (Roever, 1964), and in hundreds of instances in the bot fly *Cuterebra latifrons* on hilltops (Catts, 1963).

Investigative flights by milling pierids were noted. Typically when two *A. cethura* met, one chased the other, with the pursuer often becoming the pursued. Frequently other *A. cethura* and sometimes a *P. protodice* would join. Up to eight *A. cethura* were seen in such a "cloud." The two pierid species usually

followed a stereotyped, predictable pathway in approaching and flying on the summit. Marked *P. protodice* and *A. cethura* did not remain on the summit for long periods but were recaptured at intervals during the morning and early afternoon on the summit along their patrol pathways.

Investigative and chase flights against different species by perched and patrolling males frequently occurred, but interspecific battles were rarely seen. Often the other species was considerably smaller or larger or had a different color or different flight pattern. Table 7 lists some of the species that hilltopping species pursued. Investigative and chase flights of other orders of insects were noted for *P. zelicaon* (black dragonfly), *V. atalanta* (red dragonfly), *E. chalcedona* (black reduviid and black syrphid), *S. melinus* (flies, red dragonfly and yellow wasp), and *E. tristis* (flies).

The behavior of a particular *S. melinus* male with chipped wings was observed in detail for 55 minutes on October 23, 1966. The entire time he perched on a sumac bush with wings half open and did not fly except to investigate flying insects. One continuous sitting period lasted 14 minutes. He was twice seen to pass the forelegs over the eyes and antennae while twisting the head, much as flies do when "cleaning." This same individual was noted to return after one elapsed day to the same sumac bush to perch. On following days his perch area was occupied by other *S. melinus* males.

Daily Residence

Various males of hilltopping species remained on the summit for long periods of time during the day (* = undisturbed arrival and departure observed):

Species	No.	Time in continuous residence on summit (min.)
Battus philenor	1	70
*Papilio eurymedon**	1	37
P. zelicaon	1	110
*Atlides halesus**	1	82
Callophrys dumetorum	1	91
Strymon melinus	2	30, 55
Celastrina argiolus echo	1	116

Most males recaptured more than once on the same day were not observed continuously. Maximum times between when first and last collected on the summit during the day for these were:

TABLE 7. Investigative and/or pursuit flights observed among different butterfly species on Dictionary Hill

(Pursuer species listed first)

- *P. zelicaon*
  - *P. eurymedon*
  - *A. cethura*
  - *E. chalcedona*
  - *V. caryae*
  - *E. tristis*
- *A. cethura*
  - *P. zelicaon*
  - *P. protodice*
  - *A. sara*
  - *C. tullia*
- *P. protodice*
  - *P. rapae*
  - *A. cethura*
- *E. chalcedona*
  - *P. zelicaon*
  - *V. atalanta*
- *V. atalanta*
  - *V. cardui*
  - *V. caryae*
  - *V. virginiensis*
- *V. virginiensis*
  - *P. zelicaon*
  - *V. atalanta*
  - *V. caryae*
  - *S. melinus*
- *V. caryae*
  - *P. zelicaon*
  - *P. protodice*
  - *C. tullia*
  - *V. virginiensis*
  - *E. tristis*
- *S. melinus*
  - *N. antiopa*
  - *V. cardui*
  - *V. virginiensis*
  - *P. b. bernardino*
  - *E. tristis*
- *S. saepium*
  - *V. virginiensis*
- *C. dumetorum*
  - *E. chalcedona*
  - *Vanessa sp.*
- *E. tristis*
  - *V. caryae*

Species	Elapsed time (min.)
Anthocaris cethura	213
Pieris protodice	140
Speyeria callippe comstocki	150
Vanessa atalanta	123
V. cardui	12
V. caryae	87
V. virginiensis	82
Leptotes marina	25
Erynnis tristis	45

An attempt was made on May 16, 1966, to recapture *Euphydryas chalcedona* males in the afternoon that were marked in the morning. *E. chalcedona* were marked and recaptured during two 80-minute periods, from 0800-0920 and from 1223-1343 hours. Thirty-one individuals were marked, 19 in the morning and 12 in the afternoon. Only about 10 individuals were seen that were not marked. Five specimens were recaptured: after 15, 44, 50, 246, and 318 elapsed minutes. Only two from the morning period were recaptured in the afternoon. The data suggest that there was a high rate of turnover during the course of the day.

One marked *P. zelicaon* male was seen in territorial behavior on the summit on eight different days over a 20-day period (December 19, 1966, to January 8, 1967). This male frequented a particular area on the south side of the summit from which it "attacked" other male *zelicaon* in battles and pursuit flights. Fig. 9 is a summary of the times during the day it was observed.

Numbers of specimens recaptured at different times on a given day (after at least ten minutes of elapsed time) on summits during this study are as follows:

Battus philenor	1
Papilio eurymedon	13
P. indra pergamus	3
P. rudkini	5
P. zelicaon	66
Anthocaris cethura	29
Pieris protodice	13
P. sisymbrii	4
Euphydryas chalcedona	13
Speyeria callippe comstocki	3
Vanessa atalanta	7
V. cardui	2
V. caryae	1

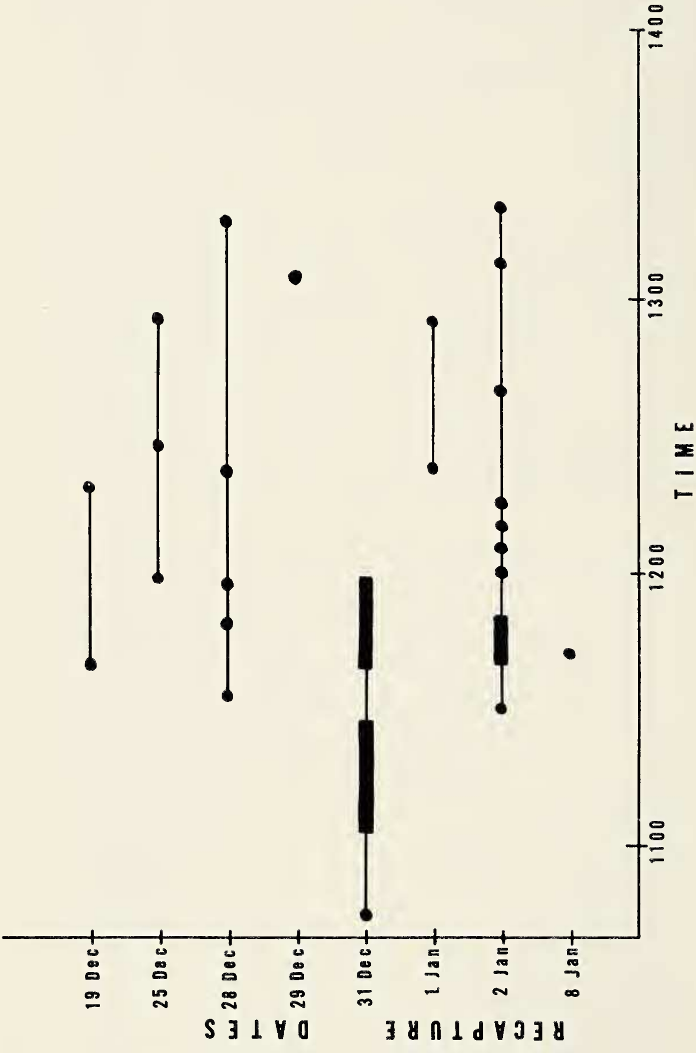

Fig. 9. Summary of times when a marked male *Papilio zelicaon* was observed over a 20-day period on Dictionary Hill summit. Dots represent individual recaptures and bars represent periods when continuously seen.

V. virginiensis	5
Atlides halesus	3
Callophrys dumetorum	9
Celastrina argiolus echo	8
Leptotes marina	1
Strymon melinus	3
Erynnis tristis	2

These numbers indicate that at least a substantial number of hilltopping males remain for periods of time on a summit on a given day.

Daily arrival as reflected by continuous collecting on a summit on a given day was determined for *Papilio zelicaon, P. eurymedon,* and *Anthocaris pima* (Table 8). In each case a majority arrived within the first hour after the first individual for the day had arrived, with the remainder arriving two to two-and-one-half hours after the first hour.

Diurnal Periodicity

Initial sightings of males in hilltopping activity were observed for the four *Vanessa* species. These first flew to the summit to hilltop only in the afternoons between 1220 and 1515 hours. Generally all four species were present on a given day. On six days, two to three of the species initially hilltopped together. The first species to be sighted in hilltopping behavior varied from day to day:

First species	No. days
V. atalanta	19
V. virginiensis	15
V. cardui	12
V. caryae	11

Only the first *Vanessa* of the day to remain onthe summit in circling, aggression, and alighting behavior was recorded; those individuals feeding or flying over the summit were not considered.

For these *Vanessa* males, time of initial sighting, ambient air temperature, and relative humidity were recorded on 51 days during various times of the year. The time of initial sighting is correlated with air tempertaure and relative humidity (Fig. 10). The warmer the air temperature, the later they will arrive; the cooler it is, the earlier they will arrive. If the temperature remains constant, they would arrive earlier with decreasing relative humidity and later with increasing relative humidity. No correlations were apparent when relative humidity was plot-

TABLE 8. Daily arrival reflected by continuous collecting of butterfly species on a summit

Species, place, date	Total males	1000-1030	1030-1100	1100-1130	1130-1200	1200-1230	1230-1300	1300-1330	1330-1400	1400-1430
Papilio zelicaon Dictionary Hill, California February 4, 1967	20	0	11	3	1	2	0	3	-	-
Papilio zelicaon Dictionary Hill, California February 12, 1967	28	0	7	6	3	2	3	5	2	-
Papilio eurymedon Tecate Mountain, California April 9, 1967	23	9	3	3	3	3	0	2	-	-
* *Anthocaris pima* "A" Mountain, Arizona March 2, 1960	96	0	0	15	35	27	6	11	2	0

*Collected by K. Roever.

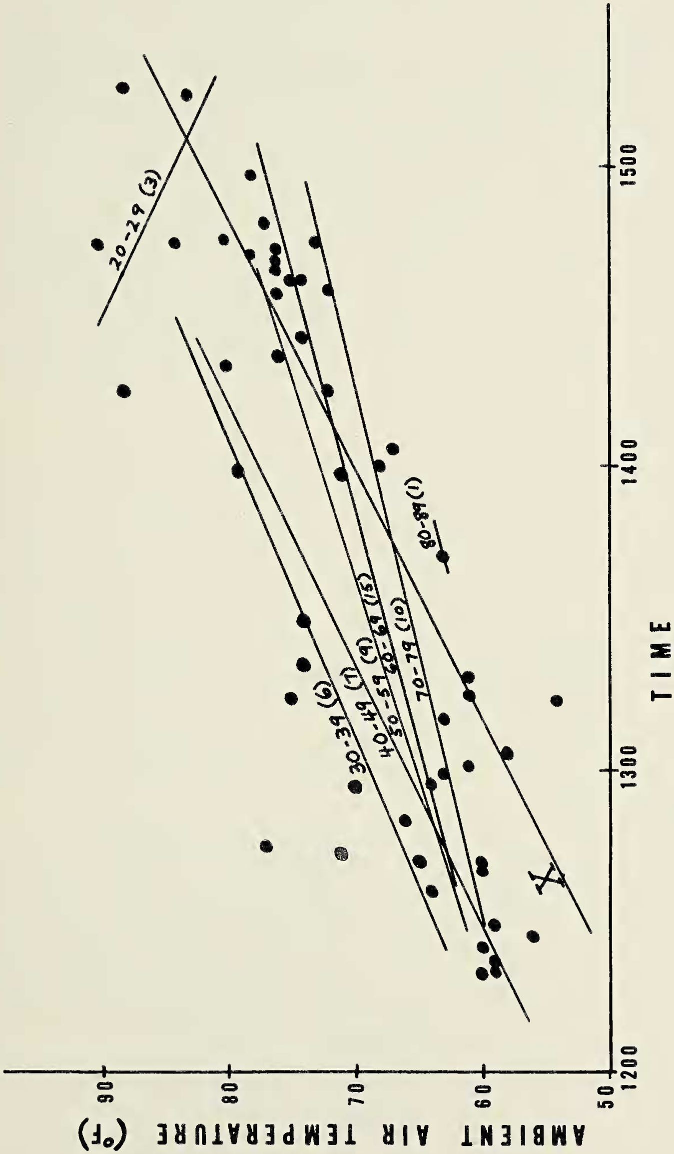

Fig. 10. Initial sightings of hilltopping *Vanessa* species. Linear regression lines by least squares are computed for a relative humidity in 10% intervals. Line "X" is the mean of all points. Time is adjusted to local apparent noon.

ted against time and when air temperature was plotted against relative humidity. Wind velocity, amount of overcast, and barometric pressure were not considered but may also be influencing factors.

Migration

Butterfly migrations have occasionally been reported to pass over summits of hills and mountains. Species reported include *Vanessa cardui* (Fritsch, 1879; Wright, 1906:37), *Danaus plexippus* (Edwards and Scudder, 1877), and a *Delias* species (Poulton, 1921, 1922). In these instances no "staying" behavior at the hilltop was shown by the migrants. A migration of *V. cardui* to the north on Dictionary Hill on March 30, 1966, behaved much as Wright (1906:37) described. Specimens flew upslope from the south, flew across the summit, and kept flying up and out off the north slope instead of proceeding downhill. Other individuals were noted to pass over the hill's shoulders. No concentration toward the summit by the flight was noted.

Mark-Recapture Study

Fourteen hilltopping species comprising 968 males were marked on Dictionary Hill summit. The percentage of recaptures after one elapsed day for these species varied from 0 to 38 percent with a mean of 13.5 percent (Table 9). For comparison with another hilltop, six hilltopping species were marked and recaptured on Two Mile Hill in a desert environment (Table 10). On Dictionary Hill, *P. zelicaon, A. cethura,* and *C. dumetorum* had the highest percentages of recapture and the four *Vanessa* species had the lowest. The low rate of recapture for *Vanessa* species was probably due to the difficulty of capturing these and the large numbers of individuals of *Vanessa* present on any one day.

Catts (1963) found that resightings of marked males of the hilltopping bot fly *Cuterebra latifrons* on a hilltop was 25.7, 29.5, and 33.3 percent over a three-year period. Apparently no mark-recapture work with hilltopping butterflies has been done besides Shepard's work (1966) with *Pieris occidentalis.* Results of marking butterflies from non-hilltop areas are summarized in Table 11.

The elapsed days from marking to recapture for eight species on Dictionary Hill summit are summarized in Table 12. It is evident that these species often return to the summit after a number of days have passed. There is some evidence that certain males may spend their entire life on the summit, judging from certain individuals that had fresh wing condition when

TABLE 9. Mark-recapture results for male butterflies on Dictionary Hill summit (on 95 different days)

Species	Number marked	Number recaptured	0/0 Recaptured after one/more elapsed days	Longest no. days to recapture
Papilio zelicaon	389	126	32.4	29
Papilio eurymedon	11	1	9.1	1
Anthocaris cethura	64	17	26.6	14
* Pieris protodice	66	10	15.2	6
Euphydryas chalcedona	144	22	15.3	10
Speyeria callippe comstocki	31	4	12.9	17
Vanessa atalanta	53	2	3.8	3
Vanessa cardui	46	0	0.0	-
Vanessa caryae	47	1	2.1	2
Vanessa virginiensis	18	1	5.6	1
Callophrys dumetorum	24	9	37.5	18
Strymon melinus	37	3	8.1	4
Celastrina argiolus echo	11	1	9.1	8
Erynnis tristis	27	3	11.1	4
	968	200		

*This compares well with Shepard's (1966) findings on Slate Peak, Washington, for closely related species:

Pieris occidentalis	41	6	14.6	14

TABLE 10. Mark-recapture results for male butterflies on Two Mile Hill summit, Scissors Crossing, San Diego County, California (on three different days)

Species	Number marked	Number recaptured	0/0 Recaptured after one/more elapsed days
Papilio rudkini	15	4	26.7
Anthocaris cethura	8	5	62.5
Pieris protodice	2	0	*
Pieris sisymbrii	15	1	6.7
Callophrys dumetorum	2	1	*
Atlides halesus	1	1	*
	43	12	

* Insignificant amount to compute percent.

TABLE 11. Mark-recapture results from other sources for butterfly species

Species	Number marked	Number recaptured	0/0 Recaptured after at least one day	Habitat	Source
Papilio glaucus	49 (46m, 3f)	17	34.7	Feeding area	Fales, 1959
Parnassius phoebus	--	--	60.0	--	Shepard, 1966
Anthocaris sara	68 (males)	17	25.0	Canyon bottom	Evans, 1955
Euchloe ausonides	--	--	10.0	--	Shepard, 1966
Maniola jurtina	1565**	183	11.7	Meadows	Dowdeswell, Fisher, and Ford, 1949
Erebia epipsodea	--	--	25.0	Meadows	Shepard, 1966
Euphydryas editha	185 (mostly males)	97	52.4	Sedentary around foodplant	Ehrlich, 1961
Hamadryas guatamalena	9 (7m, 2f)	2	22.2	On tree trunks	Ross, 1963
Vanessa atalanta	67 (prob. males)	8	11.9	In garden	Fletcher, 1936
Vanessa cardui	7	1	14.3	In garden	Fletcher, 1936
Plebejus icarioides	--	--	33.0	Around foodplant	Shepard, 1966
Polyommatus icarus	330	86	26.1 (minimum value)	On small island	Dowdeswell, Fisher, and Ford, 1940
Catocala (moths), 16 species	314	30	9.1	On tree trunks	Brower, 1930

Dashes represent unknown.

** Sexes not differentiated

TABLE 12. Elapsed days from marking to recapture for certain hilltopping species on Dictionary Hill, including separate entries for specimens taken on two or more different days.

Number days	*P. zelicaon*	*A. cethura*	*P. protodice*	*E. chalcedona*	*S. callippe*	*C. dumetorum*	*S. melinus*	*E. tristis*
1	38	1	6	6	1	3	1	1
2	18	5		6			1	2
3	13	5	3	5			3	
4	16	2	1	3	1	1	1	1
5	15	2		2		2		
6	4		1					
7	22	1		3	2	2		
8	16	2		4		1		
9	8	1			2	2		
10	8			1				
11	1							
12	3							
13	7					1		
14	5	1						
15	4							
16	1				1			
17					1			
18	1					1		
19	3							
20	2							
21-26 (none)								
27	1							
28	2							
29	1							
total specimens recaptured	126	17	10	22	4	9	3	3
no. taken > once	35	3	1	6	2	4	2	1
0/0 of recaptures taken > once	27.8	17.6	10.0	27.3	*	44.4	*	*

* = entry not very significant.

first marked and had extremely worn wing condition and weak flight when finally recaptured.

Papilio zelicaon Release Experiments

One hundred and forty-three male *P. zelicaon* collected on the summit of Dictionary Hill were marked and released at various distances and degrees of the compass to see if they would "home in" on the summit (see Table 13 and Fig. 11). One-third did return, about the same percentage that were marked on the summit and were recaptured there. In one instance two males that returned from the north also returned to the summit when released from the south. One male that was released nearly three miles away flew into a wind to return.

P. zelicaon released far away from the summit homed in on a nearby hilltop. Ten male *P. zelicaon* and one male *P. eurymedon* collected on the summit of Dictionary Hill were transported four miles to the northeast and released. Two of the *P. zelicaon* and the *P. eurymedon* homed in on the summit of a hill 997 feet high 3,400 feet to the southeast of the release point. Three of 19 *P. zelicaon* males transported to the desert about 40 air miles away hilltopped on "Two Mile Hill" about one mile to the northwest of the release point.

There is some evidence that *P. zelicaon* males will return to their own hill when given a choice of hills. Two groups of males, one group from the summit of Dictionary Hill and the other from the summit of a hill 924 feet high and 2,200 feet southeast of the summit of Dictionary Hill, were released together at location number 12 (Fig. 11):

Date released	No. released	No. recapt.	Elapsed days to recapture
III-19-67	6 (from Dictionary)	4	1, 1, 1, 6
	5 (from 924′)	1	1
IX-27-67	4 (from Dictionary)	3	1, 1, 1
	1 (from 924′)	1	1

On both dates all the recaptures were from the hilltop where the specimen was originally collected. The specimen collected on Hill 924 on September 28, 1967, was released on the summit of Dictionary Hill and returned the next day to the summit of Hill 924.

Minimum speed of return to the summit of Dictionary Hill was estimated for four *P. zelicaon* males that were recaptured on the same day:

TABLE 13. Marked male Papilio zelicaon recaptured on top of Dictionary Hill after relaease away from the summit (see Fig. 12)

No. of location	Distance from summit (ft) Vertical	Horizontal	Date released	Number released	Number recaptured	Elapsed days to recapture
1	765	7,200	I-14-67	13	5	1,1,1,1,12
2	640	5,500	II- 5-67	5	2	6,7
3	595	14,000	II-11-67	11	1	1
4	715	6,400	I- 8-67	6	4	1,1,1,1
5	715	7,900	II- 4-67	10	2	1,18
6	685	4,000	I-29-67	5	2	4,6
9	365	5,000	II- 2-67	4	3	2,2,2
10	285	4,400	II- 4-67	10	1	1
11	205	1,200	III- 2-67	1	1	5
12	265	2,600	I- 7-67	5	4	1,1,2,2
			I- 9-67	7	1	1
			II-13-67	27	7	0,0,0,3,7,9,27
			II-28-67	2	1	7
			III-12-67	3	0	-
			III-16-67	2	0	-
			III-19-67	6	4	1,1,1,6
			III-20-67	10	2	5,5
			IX-27-67	4	3	1,1,1
13	365	1,800	II-16-67	5	4	4,4,4,10
14	665	7,600	XII-24-67	2	0	-
			XII-26-67	5	1	0
				143	48	

recapture = 33.6 0/0

Specimens released at locations 7, 8, and 9 were recaptured on the summit of the 842 foot hill (distance = feet from summit of 842 foot hill):

7	560	3,200	I-27-67	8	1	8
8	300	3,200	I- 8-67	5	1	1
9	140	3,800	II- 2-67	4	1	1

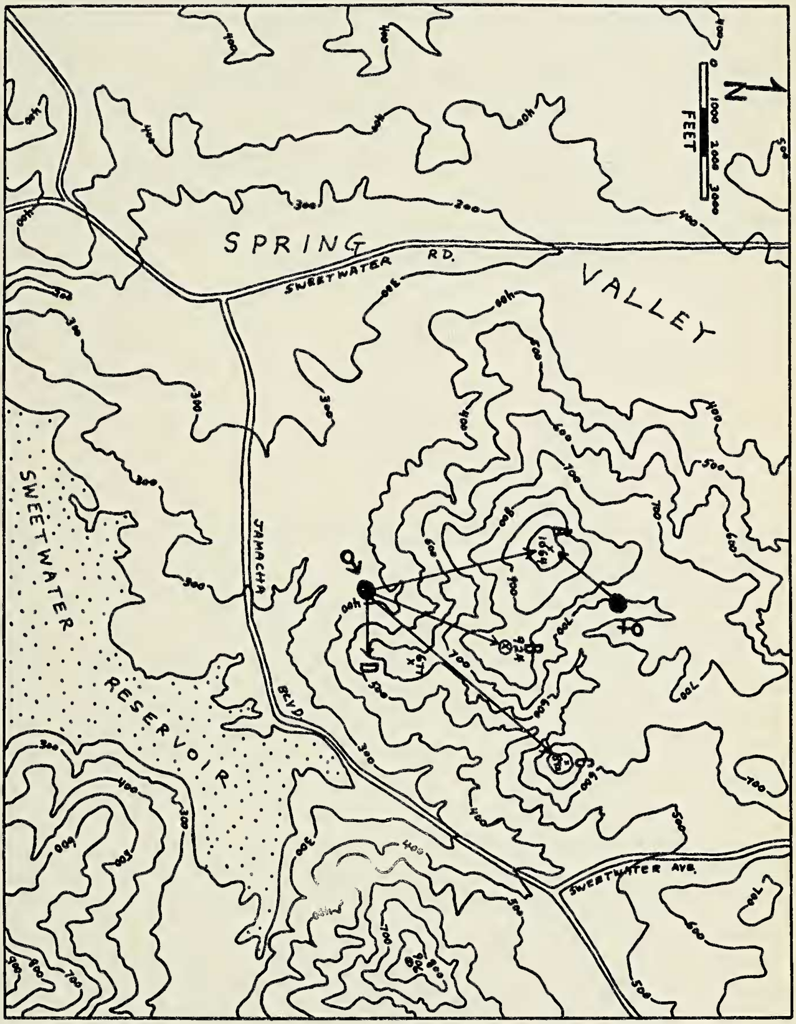

Fig. 11. Release points for reared female (♀) and male (♂) *Papilio zelicaon* and the summits they "homed in" on: A = Dictionary Hill, B = Hill 924, C = Hill 842, D = crest near Hill 677.

Distance travelled (ft.)	Time elapsed (min.)	Speed (ft./min.)
(1) 7,200	155	47
(2) 2,600	34	76
(3) 2,600	31	84
(4) 2,600	19	137

Specimen (1) travelled the distance when no wind was blowing, and specimens (2)-(4) travelled at right angles to a strong westerly wind.

Eighty males from the stock used in the *Papilio zelicaon* female release experiment shortly to be discussed, were released on February 21, 1968, at location 6 (Fig. 12). Twenty-one (26.3%) of these were recaptured on nearby summits:

Location	Vertical feet	Horizontal feet	No. recapt.	Elapsed days to recapture
A	685	4,000	11	2, 2, 2, 2, 2, 3, 3, 3, 3, 4, 4
B	545	3,200	5	4, 7, 7, 11, 18
C	460	5,500	1	9
D	220	1,300	4	7, 7, 8, 8
			21	

Each recaptured male was collected and was not released back into the population. The results show that newly emerged males do not move to the same nearby summit when released from the same location. The individual at location C had to cross a ridge that blocks off location C from the release point. One wonders why the percentage of recapture (26.3%, N = 80) should be so similar to recapture for *P. zelicaon* resident males released away from the summit (33.6%, N = 143), recaptured resident males (32.4%, N = 389), and for recaptured resident males of *Papilio rudkini* (26.7%, N = 15).

An experiment was devised to test whether or not virgin females as opposed to recently mated females seek the summit. *Papilio zelicaon* adults reared from eggs were used; the stock came from five females collected *in copula* on the summit of Dictionary Hill, January 11-14, 1968. Their progeny were reared indoors on Sweet Fennel, *Foeniculum vulgare*. Forty-five females were marked and released. Females emerged over a seven-day period prior to the release date of February 21, 1968. After emergence the adults were kept in boxes under refrigeration. One-half (22) of the females were hand-paired to wild-caught and reared males by the technique described by Clarke and Sheppard (1956) and half were left virgin. These two

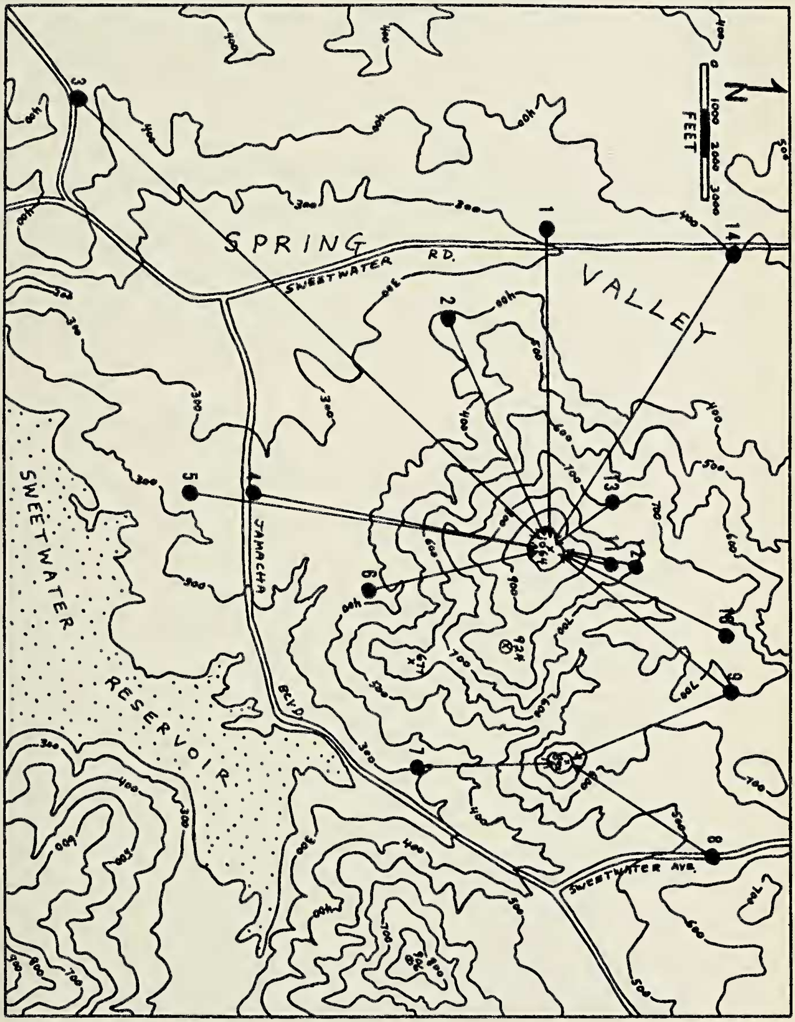

Fig. 12. Fourteen release points from which *Papilio zelicaon* males collected on Dictionary Hill summit returned to the summit of Dictionary Hill (1064 feet) and Hill 842 (842 feet).

groups were released together late in the afternoon 2,000 feet (385 vetrical feet) to the northeast of the summit (Figure 11). During the subsequent four days the summit was intensively collected; the results were as follows:

Date	No. females unmated	No. females mated
Feb. 22	10	1
Feb. 23	3	1
Feb. 24	0	0
Feb. 25	0	1
	13	3

In other words, 59.1 percent of the virgin females and only 13.6 percent of the mated females were recaptured, yet all of these 16 recaptured females proved to be virgin when dissected. Thus the three "mated" females recaptured apparently did not adequately mate when hand-paired, but the high number of unmated recaptures suggests that the mated females not recaptured very likely received a spermatophore when hand-paired.

Percent Virginity

The percent virginity of species from non-hilltop areas varied from 0 to 30 percent, mostly under 10 percent (Table 14). In addition, T. E. Pliske kindly supplied the following unpublished data on percent virginity for species from non-hilltop areas: *Papilio palamedes,* 0.0 percent (N = 32); *P. troilus,* 0.6 percent (N = 358); *P. glaucus,* 0.0 percent (N = 171); *Ascia monuste,* 0.0 percent (N = 100); and *Danaus gilippus berenice,* 1.5 percent (N = 194). These females were randomly collected at flowers at various places in Florida during the summer of 1961. O. R. Taylor (unpublished) dissected females of many United States and Costa Rican species from non-hilltop situations and found 5 to 20 percent virginity. *Colias* virgin females constituted 10 to 20 percent of the populations (N > 100). He was able to obtain virgins of most species where the sample was greater than six.

The high percentages of virgins collected on summits (Tables 15 and 16) are in sharp contrast to samples taken in non-hilltop areas. In 21 hilltopping species where N was less than six, 15 (71.4%) were 67 percent or more virgin. The percentages of virgins in seven species, where N was nine or greater, varied from 0 to 97 percent. (There is some question whether or not *Celastrina argiolus cinerea,* whose percent virginity was zero, is a hilltopping subspecies.) Burns (letter dated June 28, 1967) says that the only virgin female *Papilio glaucus* he has examined (N > 100) came from "atop a pronounced escarpment" in Dallas County, Texas.

TABLE 14. Spermatophore counts for species collected in non-hilltop areas

Species	No. spermatophores 0	1	2	3	4	5	Number females	0/0 Virgins
PAPILIONIDAE								
+Battus philenor (Burns, 1966)	0	17	11	3	1	1	33	0.0
Papilio glaucus (Burns, 1966)	0	51	45	14	1	2	113	0.0
Papilio multicaudata	0	3	0	1	0	0	4	0.0
Papilio zelicaon	3	13	2	0	0	0	18	16.7
λ Parnassius clodius ssp.	"14"	"32"					46	30.4
λ Parnassius phoebus ssp.	"4"	"58"					63	6.5
PIERIDAE								
Anthocaris sara	0	20	2	0	0	0	22	0.0
Colias eurytheme (Stern and Smith, 1960)	1	76	16	1	0	0	94	1.1
NYMPHALIDAE								
Coenonympha tullia ssp.	8	56	4	0	0	0	68	11.8
Chlosyne acastus	0	26	1	1	0	0	28	0.0
+ Euphydryas editha (Ehrlich, 1965; Labine, 1966)	1	42	21	0	0	0	64	1.6
Poladryas pola	2	9	0	0	0	0	11	22.2
+ Speyeria callippe semivirida	2	51	2	0	0	0	55	3.8
HESPERIIDAE								
Polites sabuleti ssp.	2	32	1	0	0	0	35	6.1
Pseudocopaeodes eunus	1	24	1	0	0	0	26	4.0
							679	

Reported as new here unless otherwise indicated.

λ Spharagus present or absent; no spermatophore count made.

+ One locality only; the other species are from a number of different localities.

TABLE 15. Summary of spermatophore counts for species collected on summits

Species	Number spermatophore O(A)	1	2	3	(B) No. in copula with new spermatophore	(C) Total no. Females	[(A+B/C)] 0/0 Virgin before reaching summit
Papilio eurymedon	12	2	0	0	0	14	85.7
Papilio polyxenes asterius	0	1	0	0	0	1	
Papilio rudkini	0	2	0	0	0	2	
Papilio rutulus	1	0	0	0	0	1	
Papilio zelicaon	51	28	3	2	11	84	73.8
Anthocaris cethura	14	11	0	0	1	25	60.0
Euchloe ausonides coloradensis	0	1	0	1	0	2	
Pieris occidentalis calyce	0	0	1	0	1	1	
Pieris protodice	2	12	0	0	3	14	35.7
Pieris sisymbrii	2	1	0	0	1	3	
Chlosyne californica	1	0	0	0	0	1	
Euphydryas editha	0	3	0	0	0	3	
Euphydryas chalcedona	3	6	0	0	2	9	55.6
Speyeria callippe comstocki	1	2	0	0	1	3	
Speyeria callippe nevadensis	1	0	0	0	0	1	
Vanessa cardui	1	0	0	0	0	1	
Vanessa caryae	2	1	0	0	0	3	
Callophrys dumetorum	0	2	0	0	2	2	
Celastrina argiolus cinerea	0	12	0	0	0	12	0.0
Celastrina argiolus echo	4	1	0	0	0	5	
Incisalia iroides	3	0	0	0	0	3	
Leptotes marina	3	0	0	0	0	3	
Erynnis martialis	1	0	0	0	0	1	
Erynnis persius	3	2	0	0	0	5	
Erynnis propertius	1	0	0	0	0	1	
Erynnis tristis	23	15	0	0	14	38	97.4
Hesperia miriamae	1	0	0	0	0	1	
Hesperia uncas	2	1	0	0	1	3	
	132	110			37	242	

* Complete data in Table 16.

TABLE 16. Spermatophore counts of females of hilltopping species collected on summits *

Papilio eurymedon, 14.
Hill 997 feet, 1.7 mi. SSE El Cajon P.O., San Diego Co., Calif., II-6-67 (O). Cowles Mt., San Diego Co., Calif., VI-6-67 (O). Monument Pk., Laguna Mts., San Diego co., Calif., VI-18-60, leg. R. W. Breedlove (1); V-20-66, leg. S. K. Dvorak (O*); V-7-67 (O). Mt. Kentwood, Laguna Mts., San Diego Co., Calif., V-28-66, leg. R. W. Breedlove (1). Dictionary Hill, Iv-27-57, leg. R. W. Breedlove (O); III-7-65, leg. R. W. Breedlove (O); III-6-66, leg. S. K. Dvorak (O, O); II-5-67 (O); III-12-67 (O); Iv-22-67 (O); II-22-68 (O).

Papilio polyxenes asterius, 1.
Hill by Gates Pass, SW of Tucson, Santa Cruz Co., Ariz., II-22-66, leg. S. K. Dvorak (1).

Papilio rudkini, 2.
"Two Mile Hill," Scissors Crossing, San Diego Co., Calif., II-22-67 (1); IX-14-67 (1).

Papilio rutulus, 1.
Green Mt., Boulder Co., Colo., V-28-66, leg. J. Scott (O).

Papilio zelicaon, 84.
Monument Pk., Laguna Mts., San Diego Co., Calif., V-28-66, leg. R. W. Breedlove (1). Mt. Kentwood, Laguna Mts., San Diego Co., Calif., V-28-66, leg. R. W. Breedlove (O). Green Mt., Boulder Co., Colo., V-28-66, leg. J. Scott (1). Escalante Overlook, 7500', Dinosaur National Monument, Moffat Co., Colo., VI-9-67, leg S. Ellis (O). Dictionary Hill, II-22-66, leg. R. W. Breedlove (O); X-25-66 (1, 1); XII-17-66 (O, O); XII-18-66 (O, O, O, 1); XII-19-66 (O, O, 1); XII-24-66 (0, 0); XII-25-66 (0, 0, 0); XII-26-66 (2); XII-28-66 (0, 0, 1); XII-31-66 (O, 1*); I-1-67 (O*); 1-7-67 (O); I-9-67 (O); I-14-67 (O, O, O); I-15-67 (O, O, 3); I-27-67 (1); I-28-67 (O); II-4-67 (O, O, O, 1); II-12-67 (1); II-22-67, leg. R. W. Breedlove, (O*); II-26-67 (O, O); III-5-67 (O); III-16-67 (1); III-19-67 (1, O); IV-23-67 (O*); IV-30-67 (O); V-1-67 (O); V-4-67 (O*); IX-13-67 (1, 2, 2); IX-28-67 (O, 1*); XII-17-67 (1*); XII-22-67 (O, O*, 1*); XII-23-67 (O); XII-27-67 (1); I-1-68 (1*); I-11-68 (1*); I-13-68 (1*, 1*, 1*); I-14-68 (1*); I-21-68 (O*); I-29-68 (O); II-2-68, leg, G. Forbes (O); II-19-68 (1); II-22-68 (O); II-23-68 (O); II-24-68 (O, O, 1, 3); III-10-68 (1*). Hill 906 feet, 1.8 mi. SE Dictionary Hill, III-3-68 (O, 1).

Anthocaris cethura, 25.
Dictionary Hill, II-12-67 (1); II-20-67 (O); II-28-67 (1, 1); III-5-67 (O); III-12-67 (1); III-16-67 (O*) III-25-67 (1); IV-8-67, leg. R. W. Breedlove (O, O); Iv-22-67 (O);

TABLE 16 (continued)

IV-23-67 (O); IV-27-67 (O); V-4-67 (O); V-14-67 (O); II-22-68 (1); II-23-68 (O); II-25-68 (1); II-26-68 (1); leg. S. K. Dvorak, III-21-68 (1). Tectate Mt., San Diego Co., Calif., IV-9-67 (O); V-20-67 leg. R. W. Breedlove (1). Hill 997 feet, 1.7 mi. SSE El Cajon P. O., San Diego Co., Calif., IV-27-58 (1); III-15-59 (O); III-21-59 (O).

Euchloe ausonides coloradensis, 2.
East end of S. Table Mt., Jefferson Co., Colo., V-20 to 22-66, leg. J. Scott (1, 3).

Pieris occidentalis calyce, 1.
Ridge above Cottonwood Pass, Chaffee Co., Colo., VII-26-67 (2*).

Pieris protodice, 14.
Dictionary Hill, XII-17-66 (1); XII-19-66 (1, 1); XII-28-66 (1); XII-29-66 (O); I-15-67 (1); II-2-67 (1); II-20-67 (1*); III-30-67 (1); V-14-67 (1); VI-9-67 (1); I-13-68 (O). Hill 842 feet, E. of Dictionary Hill, I-9-67, leg. F. T. Thorne, (1). Tecate Mt., San Diego Co., Calif., V-20-67, leg. F. T. Thorne, (1).

Pieris sisymbrii, 3.
Mt. Kentwood, Laguna Mts., San Diego Co., Calif., IV-30-66, leg. S. K. Dvorak (1*); V-7-67 (O). Tecate Mt., San Diego Co., Calif., III-28-64, leg. S. K. Dvorak (O).

Chlosyne californica, 1.
"Two Mile Hill," Scissors Crossing, San Diego Co., Calif., II-18-67 (O).

Euphydryas editha, 3.
Dictionary Hill, III-30-67 (1); II-23-68 (1, 1).

Euphydryas chalcedona, 9.
Dictionary Hill, II-26-67 (O); III-19-67 (1); IV-17-67 (1, 1*,); IV-27-67 (O); V-2-67 (1); V-6-67 (1*); V-14-67 (1). Tecate Mt., San Diego Co., Calif., IV-9-67 (O).

Speyeria callippe comstocki, 3.
Dictionary Hill, IV-16-67 (O); V-14-67 (1). Cowles Mt., San Diego Co., Calif., VI-6-67 (1*).

Speyeria callippe nevadensis, 1.
Buckskin Mt., Santa Rosa Range, Humboldt Co., Nev., VIII-11-67 (O).

Vanessa cardui, 1.
Dictionary Hill, I-6-67 (O).

Vanessa caryae, 3.
Dictionary Hill, III-5-67 (O); V-1-67 (1); V-14-67 (O).

Callophrys dumetorum, 2.
Dictionary Hill, III-16-67 (1*); III-25-67 (1*).

TABLE 16 (continued)

Celastrina argiolus cinerea, 12.
Green Mt., Boulder Co., Colo., V-30-65 (1, 1, 1, 1, 1); V-25-66 (1, 1); V-28-66 (1, 1, 1, 1, 1); all leg. J. Scott.

Celastrina argiolus echo, 5.
Dictionary Hill, IV-22-67 (O); V-6-67 (O*). Hill 842 feet, E. of Dictionary Hill, II-4-67, leg. R. W. Breedlove (O). Tecate Mt., San Diego Co., Calif., IV-29-61 (O); IV-23-66, leg S. K. Dvorak (1).

Incisalia iroides, 3
Dictionary Hill, II-13-67 (O); IV-23-67 (O); II-24-68 (O).

Leptotes marina, 3.
Dictionary Hill, III-30-67 (O*); IV-16-67 (O); IV-27-67 (O).

Erynnis martialis, 1.
Green Mt., Boulder Co., Colo., V-28-66, leg. J. Scott (O).

Erynnis persius, 5.
Hilltop, Coal Creek Canyon, Jefferson Co., Colo., VI-6-65, leg. J. Scott (O, O, 1). Genesee Mt., Jefferson Co., Colo., VI-10-66, leg. J. Scott (1). Wildcat Mt., Douglas Co., Colo., V-21-67, leg. J. Scott (O).

Erynnis propertius, 1.
Dexter Pk., Cuyamaca Mts., San Diego Co., Calif., V-7-67, leg. R. W. Breedlove (O*).

Erynnis tristis, 38.
Hilltop 997 feet, 1.7 mi. SSE El Cajon P.O., San Diego Co., Calif., II-6-67 (O, O*, 1*). Dictionary Hill, I-15-67 (O); I-26-67 (O); I-27-67 (1); II-2-67 (O*, O*, O*, 1*); II-4-67 (O, O*, 1*); II-5-67 (O); II-11-67 (1*, 1*); II-16-67 (O); II-22-67 (1*, 1*); II-26-67 (O, *O*, O*, 1*, 1*); II-27-67 (O,* 1,* 1*); II-28-67 (1*); III-16-67 (O*, O*, 1*); V-14-67 (O); II-22-68 (O*); II-23-68 (O*, O*); II-24-68 (O*); II-25-68 (O*, 1*).

Hesperia miriamae, 1.
Unicorn Pk., Yosemite National Park, Calif., VIII-12-58 (O*).

Herperia uncas, 3.
Hilltop 4 mi. S. of Gunnison, Gunnison Co., Colo., VII-2-67 (O); VII-20-67 (O, 1*).

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* Each number in parentheses is the number of spermatophore(s) for an individual female. These were collected by me unless otherwise indicated. Those with an asterisk were taken in copula.

This high percentage of virgins is what one would predict if summit congregations serve a meeting purpose for the sexes, since non-virgins in species that mate but once would not seek summits to mate. Single mating exists in certain butterflies in eastern North America (Burns, 1966). However, one would also expect that non-virgin females might also seek summits in species that mate more than once, as in *Papilio* (Burns, 1966), and *Euphydryas* (Labine, 1966). It is significant that the three lowest percentages (excluding *Celastrina argiolus cinerea*) of virgin females on summits (36, 56, and 60) were for species that were seen to oviposit on and near the summit as well as in other areas, so that ovipositing and mate-seeking females were probably both present on the summit in these species.

Non-hilltopping species were rarely encountered on summits (Tables 17 and 18). The only such species taken in numbers, *Anthocaris sara* (N = 18) and *Pieris rapae* (N = 10), showed no virginity, as did four of the six other species.

Female Rarity

It is evident from marking experiments that males of *Papilio zelicaon* will remain for long periods of time on the summit on a given day and will return to hilltop for a number of days. Presumably, virgin females will arrive at the summit for one day only, and then only long enough to mate. Females of *in copula* pairs watched until they uncoupled always flew downhill a short time after termination of copulation. On a given day one would expect a lower number of females than males to be present on the summit, assuming that both sexes are emerging from pupae in about equal numbers over an extended period of time. Butterflies apparently do emerge in about one-to-one sex ratio (Table 19). During periods of low male density, the females would be more easily noticed than during periods of high male density because *in copula* pairs would be more rapidly formed when many males are territorial. *In copula* pairs were mostly found by observing initial courtship; few were discovered already *in copula*. Most pairs mate downslope after flying from the summit and are difficult to locate because of the large area to search for them.

A comparison of the number of females of *P. zelicaon* present with the number of males marked and recaptured during periods of low and high density was made over two 30-day periods. During December 17, 1966 to January 15, 1967, there was a period of low male density; 57 were marked on 18 different days. During that time 29 females were captured and three were

TABLE 17. Summary of spermatophore counts for non-hilltopping species

Species	Number spermatophores O(A)	1	2	3	(B) No. in copula with new Spermatophore	(C) Total no. females	[(A+B)/C] 0/0 Virgin before reaching summit
Anthocaris sara	0	16	2	0	0	18	0.0
Zerene cesonia	0	1	0	0	0	1	
Eurema nicippe	0	2	0	0	0	2	
Pieris rapae	0	9	1	0	0	10	0.0
Coenonympha tullia	0	1	0	0	0	1	
Chlosyne gabbi	1	0	0	0	0	1	
Everes comyntas	0	2	0	0	0	2	
Erynnis funeralis	1	3	0	0	0	4	
	2	37			0	39	

TABLE 18. Spermatophore counts of females of non-hilltopping species collected on summits

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Anthocaris sara, 18.
Dictionary Hill, San Diego Co., Calif., IV-10-66, leg. R. W. Breedlove (1); II-12-67 (1, 1); II-27-67 (2, 1); II-28-67 (2); IV-30-67, leg. R. W. Breedlove (1); V-14-67 (1, 1, 1, 1); V-15-67 (1, 1); II-25-68 (1, 1). Hill 842 feet, E. of Dictionary Hill, II-3-67, leg. S. K. Dvorak (1). Tecate Mt., San Diego Co., Calif., IV-28-66, leg. R. W. Breedlove (1). "Two Mile Hill," Scissors Crossing, San Diego Co., Calif., II-18-67 (1).

Zerene cesonia, 1.
Hill 906 feet, 1.8 mi. SE Dictionary Hill, IV-11-68 (1).

Eurema nicippe, 2.
Dictionary Hill, I-15-67; II-25-68 (1).

Dictionary Hill, I-15-67 (1); II-25-68 (1).

Pieris rapae, 10.
Dictionary Hill, I-19-66 (1); II-19-68 (1); II-22-68 (1); II-23-68 (1, 1, 1); II-24-68 (1); II-25-68 (1, 1, 2).

Coenonympha tullia, 1.
Dictionary Hill, II-25-68 (1).

Chlosyne gabbi, 1.
Dictionary Hill, III-30-67 (O).

Everes comyntas, 2.
Dictionary Hill, II-24-68 (1); II-25-68 (1).

Erynnis funeralis, 4
Dictionary Hill, VI-9-67 (O); II-24-68 (1); II-25-68 (1, 1).

TABLE 19. Approximate 1:1 sex ratios for butterfly species reared in numbers

Species	Number males	Number females	Source	Reference
PAPILIONIDAE				
Graphium marcellus	--	--	eggs	Heitzman, in litt.+
Papilio eurymedon	--	--	eggs	Thorne, pers. comm.
P. glaucus	24	27	eggs	Kendall, i. l.
P. indra fordi	5	5	--	Henne, p. c.
P. palamedes	30	33	eggs	Kendall, 1964
P. polyxenes asterius	24	24	eggs	Kendall, i. l.
P. rudkini	65	73	eggs	Hedges, p. c.
P. zelicaon	--	--	eggs	Thorne, p. c.
PIERIDAE				
Nathalis iole	8	8	eggs	Henne, p. c.
Pieris protodice	13	11	--	Kendall, i. l.
NYMPHALIDAE				
Asterocampa celtis	78	83	eggs	Heitzman, i. l.
A. clyton	65	74	eggs	Heitzman, i. l.
Chlosyne ismeria	124	133	eggs	Kendall, 1964
Danaus plexippus	--	--	eggs	Urquhart, 1960
Euphydryas chalcedona	--	--	eggs	Thorne, p. c.
E. editha bayensis	--	--	eggs	Ehrlich, 1965
E. phaeton	16	18	eggs	Heitzman, i. l.
Phyciodes tharos	28	24	eggs	Kendall, 1964
Polygonia interrogationis	159	143	eggs	Kendall, i. l.

TABLE 19 (continued)

Species	Number males	Number females	Source	Reference
LYCAENIDAE				
Atlides halesus	36	36	eggs	Thorne, p. c.
Calephelis perditalis	34	43	eggs	Kendall, i. l.
C. rawsoni	147	138	eggs	Kendall, i. l.
Callophrys xami	59	69	eggs	Kendall, i. l.
Incisalia henrici solatus	27	25	eggs	Kendall, 1965
Mitoura johnsoni	12	12	eggs	McCorkle, i. l.
Philotes mohave	--	--	eggs	Henne, p. c.
P. rita elvirae	--	--	eggs	Henne, p. c.
P. enoptes	--	--	eggs	Henne, p. c.
HESPERIIDAE				
Amblyscirtes linda	31	33	eggs	Heitzman, i. l.
A. vialis	14	12	eggs	Heitzman, i. l.
Copaeodes aurantiaca	16	13	eggs	Kendall, 1965
Erynnis horatius	121	111	eggs and larvae	Kendall, 1965
Gesta gesta invisus	64	71	larvae	Kendall, 1965
Megathymus yuccae	532	473	and pupae from 120 populat.	Roever, i. l.
Thorybes pylades	20	21	eggs	Kendall, 1965

"--" = numbers not available but ratio was 1:1

+ = in a letter.

sighted for a total of 32 females, or 56.1 percent of the total male population. During February 11, 1967 to March 12, 1967, there was a period of high male density; 123 were marked on 15 different days. During that time only five females were captured, or only 4.1 per cent of the total male population. Thus, during times of low density populations there may be more than half as many females as males present. Due to the difficulty of finding females *in copula,* as many females as males may actually have been present.

The population of *Papilio eurymedon* on Dictionary Hill is low in density compared to certain other summits in San Diego County, where males are frequently plentiful. Dictionary Hill is probably on the periphery of its range. During January to May 1967 only 12 different males were marked, collected, or seen on the summit, and three females were collected and one seen for a total of four females, or 33.3 percent of the total male population.

Female Behavior and Mating

Papilio zelicaon. These observations are based primarily on 77 females (58 virgin, 19 non-virgin) collected on Dictionary Hill summit. They were collected while in flight or alighted; 17 *in copula* pairs were collected and other courting and mated pairs were observed. Wing condition, as expected, showed a high correlation with mated condition; virgins almost exclusively had a fresh wing condition while most non-virgins had a fair to worn wing condition. Only one of the non-virgins had a freshly deposited spermatophore; the remainder had spermatophores that were collapsed. Frequently virgin females' genital regions were expanded when captured.

All females collected appeared on the summit during the time when males were resident and well after the males had established territories for the day. Females on the summit usually flew quite slowly; virgin females with fresh wing condition characteristically had a slow, fluttering flight, generally in areas occupied by males. When all or nearly all of the resident males were collected, females flew back and forth over the summit, occasionally alighting on the ground or vegetation; three females stayed on the summit for six, seven, and eleven minutes respectively in these lingering flights. Females that were frightened off the summit by a swing of the net flew downslope but generally returned within a few minutes.

(Edwards [1884] reported the flight behavior of a female

Papilio brevicauda on a mountain top at Topsail, Newfoundland: "It made long flights, rarely alighting, but apparently reconnoitering the whole mountain." The female was probably a virgin since she layed infertile eggs when confined.)

Virgin females, including two taken *in copula,* often had pollen adhering to their bodies and were twice noted to visit flowers before flying to the summit.

Courtship stages were seen in twelve pairs. The females flies into an area where males are perched or patrolling; the male immediately investigates her and responds by fluttering close behind her in a bobbing flight. At times this flight is done immedately in front of the female. Presumably during this flight the male is emitting a pheromone. Males as old as four weeks have a sweet pungent odor, while freshly emerged males do not. Copulation itself may take place downslope or on the summit. *In copula* pairs were found either slightly downslope (as far as 125 yards from the summit) or on the summit. The female alights at the edge of the summit or usually slightly downslope. The time the pair first meets to when their genitalia are in contact usually takes about one to three minutes. The male alights behind and parallel to the female or underneath the females and curves his abdomen until their genitalia are in contact. He then establishes a position to that each is facing in opposite directions and oriented with their backs to the sun. In most cases the female's wings are shut or partially open and the male's wings are opened flat. Pumping motions of the male's abdomen last for a few minutes. In one pair the female used her back legs to stroke the male's abdomen and genitalia intermittently. Pairs found *in copula* were resting on vegetation one to four feet off the ground (Fig. 13). The female carries the quiescent male when the pair is disturbed. The male initiates the uncoupling of the *in copula* pair.

One attempted courtship by more than one male was rejected by a virgin female. From one to four males chased the female. The female flew rapidly rather than slowly fluttering when pursued. Once a female broke into a fluttering, falling flight when closely investigated by a male *Vanessa atalanta.*

Anthocaris cethura. Fourteen females were collected on or near the summit of Dictionary Hill; of these, nine were virgins and five were non-virgins. Three females were taken *in copula.* Virgin females were mostly taken while in flight or when they had alighted in areas where males patrolled. One virgin female was collected feeding on a flower on the summit.

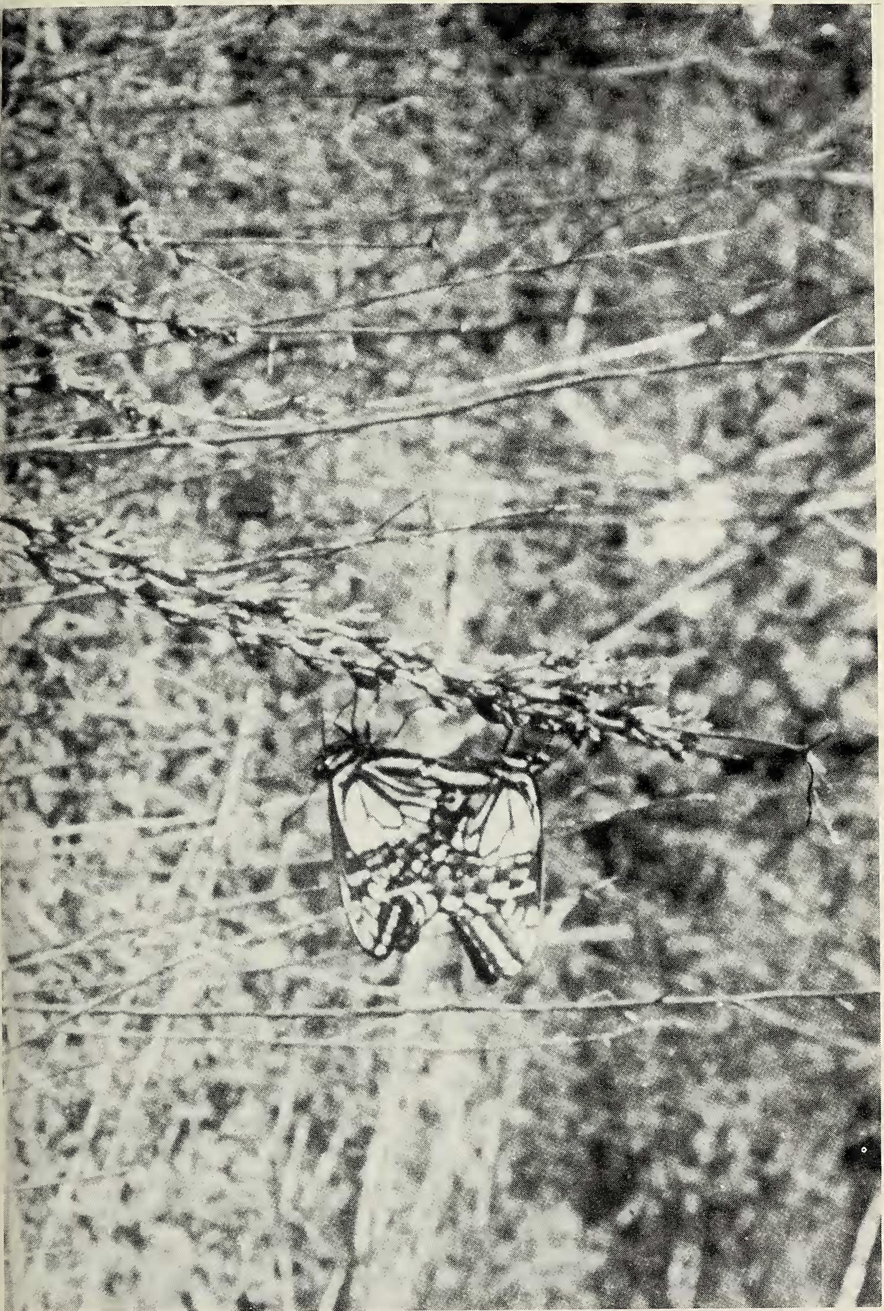

Fig. 13. *In copula* pair of *Papilio zelicaon.*

A virgin female was observed on the summit from 1009-1018 hours on April 27, 1967. During this time the female alighted four times (for periods of two minutes, three-and-one-half minutes, one minute, and one minute respectively) on vegetation in areas along a 100-foot strip where males in the past had patrolled. When perched, the female flew up to meet two passing male *Pieris protodice* and once flew up after a male *Speyeria callippe comstocki*. In both cases the *protodice* briefly courted the female but separated after five to ten seconds. At 1018 the female was collected.

A pair *in copula* was taken resting three feet up on vegetation on the summit at 1209, March 16, 1967. The female was positioned downward and the male upward. The male carried the quiescent female when the pair was disturbed. Another pair was taken *in copula* on March 21, 1968, at 1050. The female contained a collapsed speratophore indicating that she was mating for the second time.

Mating was seen with one female on February 28, 1967. At 1023 and 1102 hours fresh virgin females appeared at a rock outcropping area which males frequent on the summit. One of these was immediately collected and the other was observed. The observed female fluttered in an area with many nectar sources for about one minute and alighted on these plants without feeding. The female then alighted on some grass, perched facing upwards, and remained there, with wings shut, one foot off the ground. A marked male with fair wing condition, which had been recaptured three times on the same day, flew by the area and immediately dropped down to the female, alighting parallel to her, and initiated copulation. The female then positioned herself so that the male faced up and she faced down. The pair remained in this position with wings shut for six minutes, during which time a spermatophore was passed as shown by later dissection. Four different males, two of which were collected, flew by the area. In each case, the male suddenly dropped down to the mated pair, attempted copulation for about ten seconds, then flew off. The female may have emitted a pheromone that attracted males who were in close proximity, or the male's response may have been strictly visual. After six minutes the pair was collected.

On March 25, 1967, two non-virgin females were collected very near the summit during oviposition behavior. One oviposited on tansy mustard, *Descurainia pinnata*, a known foodplant that grows up to the summit of Dictionary Hill. The other female

hovered over black mustard, *Brassica nigra* plants, alighted on one small mustard plant, and curled her abdomen toward the plant; however, no egg was found.

Pieris protodice. Observations are based on eleven females collected on Dictionary Hill summit: two virgins and nine non-virgins. One of the virgins was captured feeding on a flower, and the other was taken *in copula.* Two of the non-virgins were taken in oviposition behavior directed toward young *Brassica nigra* plants.

Abbott (1959:288) described in detail the courtship and mating of *P. protodice* in Texas. One non-virgin female on Dictionary Hill summit displayed acceptance behavior toward a hovering male (0854, May 14, 1968): i.e., wings spread and abdomen elevated while resting on vegetation. A female with a freshly deposited spermatophore exhibited rejection behavior toward a courting male (1258, February 3, 1967, on Hill 842, east of Dictioary Hill). The female, pursued by a male, alighted on the ground. The male alighted alongside of the female and tried unsuccessfully to make genitalia contact. He then walked around in front of the female, faced her, and flew off. An *in copula* pair taken at 1058, February 20, 1967, on Dictionary Hill summit, was located because two males alighted by the pair. In two *in copula* pairs the male carried the quiescent female when the pair was disturbed.

Vanessa species. Despite numerous observations of male encounters in hilltopping *Vanessa* species, only two courtships of females were observed. This inability to observe mating pairs was probably due to the formation of *in copula* pairs in the late afternoon when few observations were made. The two courtships occurred at 1513 and 1533 hours on January 6, 1967, only two hours before sunset. *Vanessa* mating times have been reported as 4:15 p.m. for *V. atalanta,* 6 p.m. for *V. cardui* (both Pronin, 1964), and 8:30 p.m., D.S.T. for *V. cardui* (Temple, 1953). The two pairs observed in courtship were *V. cardui* and *V. caryae.* In both cases the courting pair alighted on the ground with the male behind the female and were then collected.

Strymon melinus and Incisalia iroides. No matings of these two species were observed. *I. iroides* males were only occasionally seen, but *S. melinus* males were frequently encountered in the afternoons. Again, probably the reason no matings were observed was that pairs may have formed in the late afternoons when few observations were made. Reinhard (1929) states that

S. melinus mated in Texas cotton-fields "late in the evening or shortly before sunset." Powell (1964a) noted that four pairs of *I. iroides* mated on a lemon tree only after 4:00 p.m., P.S.T.

Callophrys dumetorum. Two *in copula* pairs were collected on the summit of Dictionary Hill. At 1018, March 25, 1967, an *in copula* pair, both sexes with fresh wing condition, was found on an unopened composite flowerhead two feet above the ground. Both individuals were horizontal with wings folded, broadside to the sun. Their resting site was at the edge of a clearing where a male was exhibiting territorial behavior.

Courtship and mating were observed with a pair at 1010, March 16, 1967. A virgin female with fresh wing condition flew from the north into a male's territory on the summit. The male, which was perched and had a worn wing condition, flew up to investigate the female and hovered behind her. The female then alighted almost immediately two-and-one-half feet up on vegetation and quivered her partly opened wings. The male alighted parallel and slightly behind the female, curved his abdomen around, engaged genitalia, and positioned himself so that he faced downward and the female upward. All these actions happened rapidly. The pair faced the sun and had their wings closed. After nine minutes the pair was collected; a spermatophore had been passed during that time.

Erynnis tristis. Females were difficult to distinguish from males in flight. They were recognized as females only when *in copula* and during courtship. Essentially all of the 35 females collected on the summit were virgin and had fresh wing condition. All but one of the 14 females with freshly deposited spermatophores were taken *in copula* on the summit. All females appeared when males were actively hilltopping.

Courtship stages were seen partially or completely in six different pairs. The virgin female flies into a male's territory on the summit. The male flies off his perch to investigate the female and flutters behind and below her, occasionally rising up and making apparent contact. The female responds by alighting on vegetation one to four feet above ground (a rock in one instance served as the substrate). The male immediately alights parallel and slightly behind the female and curves his abdomen to make genitalia contact. Upon engagement the male positions himself so that he is facing down and the female faces up. Females which were closely examined at this stage had numerous scales along the shaft and nudum of their antennae. These were probably androconial scales from the male's coastal fold deposited

during the brief "contacts" before alighting. Burns (1964:88) predicted that these scales "probably serve a communicative function during courtship." The female next grasps the substrate rapidly with her legs and begins to brush off the scales along the shafts of her antennae with her front legs. Next, either the left or right leg of the female twitches rapidly, sometimes out and back and sometimes in apparent contact with the pair's genitalia region. The tip of this leg has a tuft of hairs not present on the other hind leg. I did not notice where these hairs were taken from. This leg twitching is intermittent and lasts about three minutes. Finally, the female cleans all the scales off her antennae with her front legs, at the same time rubbing her eyes and coiling and uncoiling her proboscis. The male is quiescent during all of these motions except for rhythmic contractions of his abdomen. Soon the pair ceases all motions and rests in a position about 30 degrees from the horizontal (Fig. 14). These motionless pairs could be approached quite closely, although several times such a pair took flight after prolonged close observation. Such flights extended 10 to 50 feet away, the female always carrying the quiescent male.

All of the *in copula* pairs noted (18) that were not seen in courtship were found resting in or near a known male territorial area. Frequently, passing males would investigate such a pair and attempt copulation but would leave very shortly. All pairs were perpendicular to the sun's rays. On sunny days a quiescent pair would have their wings closed, but on overcast days or during the passage of a cloud across the sun their wings were expanded.

Excessive numbers of males apparently terminated one courtship. At 1355, February 12, 1967, a female was seen pursued by two males. The female alighted several times on branches but each time flew off. A third male joined the chase when the group passed through his territory. At this point the female flew rapidly off with the three males in pursuit. Momentarily the group was lost from sight, but shortly the three males returned chasing each other. The whole encounter took about three minutes.

A rejection flight by a freshly mated female was seen at 1400, January 27, 1967. A male fluttered behind the female. The female rose high into the air, and the male rose behind her, touched her, and returned to ground level. Immediately the female returned to ground level, where the same process was repeated. The female then alighted on a bush and was collected; she contained a freshly deposited spermatorphore.

Fig. 14. *In copula* pair of *Erynnis tristis.*

Behavior of Sexes after Uncoupling

The behavior of eight *Papilio zelicaon* pairs after uncoupling on the summit was observed. If conditions were warm or mild, the females flew rapidly and continuously downhill until lost from sight; one such female was followed for one-third mile. On cool days the females unsually sunned for awhile before flying downhill; their flight was much slower with frequent alightings on vegetation to sun themselves. In all cases the females departed from the summit and did not fly around the summit like the virgin females. Departing females flew into and at random angles to the wind. Males resumed hilltopping behavior shortly after uncoupling. In one instance the male that had uncoupled from a pair 375 feet from the summit was found 20 minutes later *in copula* with another female at the summit.

Two *Erynnis tristis* pairs were observed after uncoupling on the summit on a cool, overcast day (February 19, 1968). In both cases the female sunned on the ground for several minutes before rapidly flying off the summit. With one of these pairs, arrival, copulation, and departure of the female was seen during a 61-minute period; the male resumed territorial behavior in his original territory two minutes after uncoupling.

Larval Foodplant Proximity

Tables 20 and 21 give the known larval foodplants for hilltopping and non-hilltopping species and whether they are located near or far away from the summit of Dictionary Hill. There was no difference in the percentage of hilltopping and non-hilltopping species whose foodplants were near or far, as measured arbitrarily from the 900-foot contour line (distance from the summit to the line is 400 to 1,400 feet and 164 vertical feet):

	Larval foodplant present above 900-foot contour		
	Present	Absent	% Absent
Hilltoppers	14	7	33.3
Non-hilltoppers	17	8	32.0

Certain hilltopping species had to fly a moderate distance to hilltop. *Papilio eurymedon*'s nearest foodplant source is a colony of about twenty *Rhamnus crocea* bushes 1,600 to 2,100 feet to the east (300 vertical feet). *Erynnis tristis* feeds on *Quercus agrifolia* (Burns, 1964). The nearest *Q. agrifolia* tree is 2.6 miles away, the first area of concentration is 3.1 miles away, and the main center of concentration is 3.8 miles away to the east. *Quercus dumosa* also grows in the area and may be a possible foodplant. The first bushes (five) of *Q. dumosa* are 1,900 feet away and

TABLE 20. Foodplants for hilltopping species on Dictionary Hill

Species	Larval foodplant present on slopes above 900' contour	Known possible foodplants available in the area
1. *Battus philenor*	absent	*Aristolochia* sp.
2. *Papilio eurymedon*	absent	*Ceanothus* sp., *Rhamnus californica*, *R. crocea*, *Prunus* sp.
3. *Papilio zelicaon*	absent	*Foeniculum vulgare*, *Daucus* sp.
4. *Anthocaris cethura*	present	*Descurainia* sp., maybe *Brassica nigra*
5. *Pieris protodice*	present	*Brassica nigra*, *Raphanus* sp.
6. *Chlosyne leanira wrightii*	present	*Castillija* sp. λ
7. *Euphydryas editha*	present	*Plantago Hookeriana* var. *californica*
8. *Euphydryas chalcedona*	present	*Scrophularia californica*
9. *Speyeria callippe comstocki*	present	*Viola pedunculata*
10. *Vanessa atalanta*	absent	*Urtica urens*, thistles
11. *Vanessa cardui*	present	Boraginacea, Compositae, Malvaceae (*Malva parviflora* preferred)
12 *Vanessa caryae*	present	*Malva parviflora* preferred, other Malvaceae
13 *Vanessa virginiensis*	present	*Gnaphalium* sp., other Compositae
14. *Atlides halesus*	absent	*Phoradendron flavescens*
15. *Callophrys dumetorum*	present	*Eriogonum fasciculatum*, *Lotus scoparius*
16. *Celastrina argiolus echo*	present	*Ceanothus* sp., *Lotus* sp.
17. *Incisalia iroides*	present	*Cuscuta* sp., *Ceanothus* sp., *Sedum* sp.
18. *Leptotes marina*	present	*Astragalus* sp., *Plumbago* sp.
19. *Satyrium saepium*	absent	*Cercocarpus betuloides*, *Ceanothus* sp.
20. *Strymon melinus*	present	many
21. *Erynnis tristis*	absent	*Quercus agrifolia*

Foodplants compiled from Comstock (1927), Klots (1951), Emmel and Emmel (1963b), Garth and Tilden (1963), Burns (1964), and Thorne (pers. comm.). Higgins (1949) was used as an aid to finding certain plant locations.

λ Butterfly no longer present.

TABLE 21. Foodplants for non-hilltopping species on Dictionary Hill

1.	*Anthocaris sara*	present	*Brassica nigra*
2.	*Colias eurytheme*	present	*Medicago sativa*, less frequently other legumes
3.	*Colias harfordii*	present	*Astragalus* sp.
4.	*Zerene cesonia*	present	*Amorpha* sp., *Trifolium* sp.
5.	*Eurema nicippe*	absent	*Cassia* sp.
6.	*Pieris rapae*	present	*Brassica nigra*, cultivated Cruciferae
7.	*Phoebis sennae*	absent	*Cassia* sp.
8.	*Danaus gilippus berenice*	absent	*Asclepias* sp.
9.	*Danaus plexippus*	absent	*Asclepias* sp.
10.	*Coenonympha tullia californica*	present	Gramineae
11.	*Agraulis vanillae*	absent	*Passiflora* sp.
12.	*Chlosyne gabbi*	present	*Corethrogyne* sp., *Hazardia* sp.
13.	*Junonia coenia*	present	*Plantago* sp., *Gnaphalium* sp.
14.	*Nymphalis antiopa*	absent	*Ulmus* sp., *Salix* sp., *Populus* sp.
15.	*Apodemia mormo virgulti*	present	*Eriogonum fasciculatum*
16.	*Brephidium exilis*	present	*Atriplex* sp., *Chenopodium* sp.
17.	*Everes comyntas*	present	*Astragalus* sp., *Trifolium* sp.
18.	*Glaucopsyche lygdamus*	present	*Lotus scoparius*, *Astragalus* sp.
19.	*Lycaena helloides*	absent	*Rumex* sp., *Polygonum* sp.
20.	*Philotes battoides bernardino*	present	*Eriogonum fasciculatum*
21.	*Erynnis funeralis*	present	*Lotus scorparius*, *Medicago sativa*, *Nemophila membranacea*
22.	*Heliopetes ericetorum*	present	*Malvastrum* sp., *Amaranthus* sp.
23.	*Hylephila phyleus*	absent	*Cynodon Dactylon*
24.	*Ochlodes sylvanoides*	present	Gramineae
25.	*Pyrgus communis*	present	Malvaceae

the first area of concentration is 4,600 feet away to the east. *Erynnis tristis* belongs to a superspecies of *Quercus* feeders; no other foodplants are known for the group (Burns, 1964). Freshly emerged *Papilio zelicaon* males hilltopped as far as 5,500 feet away from the release point.

Three hilltopping species were seen to oviposit on the summit: *Anthocaris cethura, Pieris protodice*, and *Euphydryas chalcedona.* Since they do oviposit as well as mate on the summit, the percentage of virgin females for these species would be less than expected if only mating took place. These three species did have the lowest percentages of virginity of the hilltopping species present (see Table 15) yet were still above the highest percent virginity for non-hilltop areas.

Species Approach to the Summit

Instances of actual flight to the summit by hilltopping species were watched for although rarely observed. Particular attention was given to local wind conditions when species did approach the summit, in view of the emphasis placed by various authors on updrafts and winds as causative agents in hilltopping.

Male *Papilio zelicaon* were twice noted at distances greater than 100 feet from the summit to approach rapidly in a straight line flight about four to five feet off the ground. In one case there was no wind noticeable; in the other case, a fair breeze was blowing at right angles to the butterfly's flight. On February 13, 1967, 27 marked *P. zelicaon* males were released 2,600 feet to the north of the summit. Three of these were recaptured on the summit about a half-hour later. During this time a steady, fresh breeze was blowing from the west, presumably at right angles to their flight paths.

Pierids were easily watched in their summit approaches because of their conspicuous white color. *Pieris protodice* males were twice noted to approach the summit from the east along a ridge and once from the south slope. These flights occurred when no breeze was noticeable and when a slight breeze was present; one flew at right angles to a breeze. *Anthocaris cethura* males mostly approached the summit of Dictionary Hill from the south or southeast slopes. One male approached the summit from the east side while a wind was blowing from the northwest. On February 18 and 21, 1967, on Two Mile Hill, many *cethura* were seen to approach the summit on the south slope while fresh breezes blew from the southeast. Like *protodice, cethura* males approached summits over a particular, stereotyped flight pathway.

The four *Vanessa* species approached the summit of Dictionary Hill from the east and sometimes from the west. Their straight approach flight, observed from the summit, changed to circling and alighting behavior once the top was reached.

Erynnis tristis males were frequently seen at the summit in apparent approach flights from the east. Only one was seen to approach from any distance from the summit. This male was seen about 200 feet down the north slope in a steady uphill fiight and became territorial on the summit one minute later.

In May of 1966 and 1967, four species were hilltopping abundantly on Dictionary Hill between 0700-0800, two hours after sunrise, when updrafts, if present, would have been slight.

In summary, approach flight by butterflies was noted both into and with winds of various strengths and at various random angles to the wind, and during times when updrafts were both maximal and minimal.

Effects of Wind at the Summit

Winds had some effect on the summit distribution of hilltopping species. Males of the four *Vanessa* species, *Papilio zelicaon*, and *Euphydryas chalcedona* were noted at times to remain on or close to the summit during fresh breezes (17-21 knots on the Beaufort Scale for wind) by flying into the wind. During these winds, hilltopping species mostly confined their activities to the leeward side. The *Vanessa* species often flew into fresh afternoon breezes blowing from the west to maintain position along the east edge of the summit. *P. zelicaon* males on Dictionary Hill often confined their hilltopping activities to the leeward side of the summit but did not buck fresh breezes to remain on the summit when the breezes were generally over the whole hill. *E. tristis* males confined their territorial activities along the east edge of the summit during west winds. Normally they spaced themselves over much of the summit.

Females of *Papilio eurymedon*, *P. zelicaon*, *Anthocaris cethura*, *Euphydryas chalcedona*, and *Speyeria callippe comstocki* flew usually quite rapidly *into* the winds in approaching or flying on the summit. One female *zelicaon* first arrived on the summit with the winds, but when blown from the summit it flew *into* the wind to return to the hilltop.

The effect of winds above the hilltop was seen when two *P. zelicaon* females were swept up high from the summit between 1130-1200 on January 15, 1967 (calm at ground level), and when a small migration of *Vanessa cardui* headed to the northeast in

the afternoon of March 30, 1966. The *cardui* flew out about 50 to 100 yards from the summit and then were carried up and out of sight; the wind was from the southwest at a steady 7 to 9 mph.

Feeding

Actual feeding on flowers by hilltopping butterflies was not often seen. Frequently species showed hilltopping activity when no flowers were available on or near the summit, such as during the fall and winter months. Perching behavior on flowers in a territory often occurred and was distinguished from feeding behavior in which the proboscis entered the flower.

Papilio zelicaon territorial males on the summit often had pollen adhering to the underside of their bodies. Eight marked male *zelicaon* captured between 1100-1400 hours had adhering pollen. These males varied from fresh to worn wing condition which suggests that feeding probably occurs throughout their life span. Occasionally males were seen feeding on flowers at at the summit before resuming hilltopping behavior. One male in the early morning was seen to leave a roosting site on the summit and to feed down the east slope without exhibiting hilltopping behavior (0725, May 9, 1967). Another male (0853, April 16, 1967), the first one to show hilltopping behavior that day, sipped water while perched on a sumac leaf. One male was seen feeding on the summit as late as 1522 (May 1, 1967); no other *zelicaon* males were seen on the summit after that time on that particular day.

Presumably male *zelicaon* feed in the morning before hilltopping and probably later in the afternoon before roosting. They may also feed away from the summit during periods of the day when actively hilltopping since certain marked males were absent from the summit at times. Some feeding by hilltopping males on the summit was seen but generally no flowers were available there. Perhaps these *zelicaon* have feeding territories, as was shown to exist in a *Papilio glaucus* population in Maryland (Fales, 1959).

Virgin females of *Papilio zelicaon* occurring on the summit, including several taken *in copula,* often had pollen adhering to their bodies. Several were seen to feed on or near the summit before performing their characteristic "circling" flight on the summit. One female fed intermittently on flowers for 30 minutes on the north slope about one-quarter mile from the summit; it had an uncollapsed spermatophore in the bursa. This particular female had no pollen adhering to its body; thus individuals

taken on the summit with no pollen could still have fed. Virgin females apparently feed for a time after pupal emergence before seeking the summit to mate.

The *Vanessa* species fed extensively on flowers in the morning in home gardens surrounding Dictionary Hill, especially on lantana. At 1150 on April 13, 1966, many *Vanessa* individuals fed on yellow composites on the north slope, but none were hilltopping up to the departure time of 1310. Occasionally *Vanessa* individuals fed on or near the summit but always before starting their afternoon hilltopping behavior. One *V. caryae* male fed on the summit as early as 0725, two hours and twelve minutes after sunrise (May 2, 1967) when the temperature was 54°F. During the height of *Vanessa* hilltopping activity, individuals did not feed, although when they began to hilltop there was some overlap of feeding individuals and hilltopping individuals.

Numerous *Euphydryas chalcedona* males on the summit were sometimes seen feeding on yellow composites and at the same time displaying aggression toward each other and passers-by. One mated female was collected while feeding on the summit.

Other species noted feeding on the summit included a male and a virgin and mated female of *Anthocaris cethura*, a male and a virgin female of *Pieris protodice*, a female *Pieris rapae*, a male *Speyeria callippe comstocki*, a female *Chlosyne gabbi*, a virgin female *Leptotes marina*, a male *Callophrys dumetorum* (feeding in its territorial area), two male *Erynnis tristis*, and a male *Erynnis funeralis*.

Roosting

Crane (1967) mentions that five species of *Heliconius* in Trinidad roost gregariously, the same individuals returning to the same bushes or vines on successive nights. McFarland (1965) says that the lycaenid *Callophrys macfarlandi* roosts in clumps of *Nolina*, its foodplant. *Ministrymon leda* also roosts on its foodplant (Mesquite) in southern Arizona. Such gregarious roosting and foodplant roosting were not noticed on the summit of Dictionary Hill. Rau & Rau (1916:251-257) describe sleep postures of some butterflies and include an annotated bibliography on the subject. Roever (personal communication) says that *Vanessa* species roost in palo verde trees on the summit of "A" Mountain near Tucson, Arizona.

The vegetation on the summit of Dictionary Hill is extensive so that roost sites were difficult to locate. During April and May,

1967, eleven attempts were made to locate species roosting by inspecting the summit early in the morning and late in the afternoon. Both hilltopping and non-hilltopping individuals were found roosting. Non-hilltopping individuals included a male *Nymphalis antiopa*, two female *Euphydryas chalcedona*, and a female *Papilio zelicaon* (all three females contained spermatophores). Roosting males of hilltopping species included two *Vanessa atalanta*, one *V. cardui*, one *Speyeria callippe comstocki*, one *Euphydryas chalcedona*, and 14 *Papilio zelicaon;* these roosted mostly in weeds along the edge of the summit. The one *E. chalcedona* male and four of the *P. zelicaon* males were recaptures from previous days. One *P. zelicaon* male was recaptured roosting on three successive mornings along a 55-yard strip of weeds. On April 30 this specimen sunned itself at 0940 and was captured in hilltopping behavior at 1020. Roosting specimens were found most often in the early morning on the summit vegetation with closed wings or with wings open to sun themselves. *P. zelicaon* males when disturbed from sunning positions flew quite rapidly and alighted again on vegetation almost immediately.

Many hilltopping species of flies were noted roosting on the summit on Broom Baccharis. Catts (1963) found that at least some *Cuterebra latifrons* (Cuterebridae) males spent the night in chaparral on a hill summit and resumed territorial behavior on the summit at temperatures of about 19° C. Catts (1964), working with the oestrid flies *Cephenemyia apicata* and *C. jellisoni*, mentions that males roosted in and near hilltop aggregation sites.

Predation

Knudsen (1954) reported several hundred butterflies of three hilltopping species in an area of a few hundred square feet on the summit of Kennesaw Mountain, Georgia, and Waterhouse (1932) collected over 300 butterflies of three species on top of Kosciusko in Australia in one day. About 25 to 100 butterflies are usually encountered on a given day during late February, March, and April on the summit of Dictionary Hill. Concentrated predation on such large numbers of butterflies was expected but not seen. *Vespula* wasps have been known to prey on a hilltop swarm of winged ants (Chapman, 1963), and there is a report of sparrows attacking a "mud-puddle club" of *Papilio glaucus canadensis* (Rawson & Bellinger, 1953), but no such attacks were observed during this study.

Predators reported attacking adult butterflies include the following: robber flies (Fryer, 1913; Dover, 1920; Field, 1938; Klots, 1951; Price, 1961), dragonflies (Scudder, 1889; Fryer, 1913; Dover, 1920; Field, 1938; Klots, 1951; Price, 1961), Hymenoptera (Scudder, 1889; Ford, 1957), Hemiptera (Field, 1938; Macy & Shepard, 1941; Klots, 1951), mantids (Field, 1938), crab spiders (Field, 1938; Klots, 1951; Voss, 1953), web weaver spiders (Klots, 1951), frogs (Klots, 1951; Price, 1961), toads (Klots, 1951), lizards (Dover, 1920; Annandale & Dover, 1921; Field, 1938; Klots, 1951; Ford, 1957), tree-snakes (Dover, 1920; Annandale & Dover, 1921), many different birds (Scudder, 1889: 1612; Fryer, 1913; Dover, 1920; Annandale & Dover, 1921; Carpenter, 1937, 1941a,b; Field ,1938; Klots, 1951; Knowlton, 1953; Ford, 1957; Urquhart, 1960:209; Olson, 1962; Petersen, 1964), bats (Field, 1938), chipmunks (Morris, 1953), and monkeys (Field, 1938; Klots, 1951).

During this study no butterfly predation was seen. However, certain potential predators such as lizards and birds were occasionally present on the summit of Dictionary Hill. Also, territorial male butterflies often had beak-marks or "beak injuries" from birds (see Carpenter, 1937), although such predation attempts may have occurred away from the summit.

A flycatcher (*Myiarchus cinerascens*) was sighted on eight different days over a 25-day period (presumably the same individual). The bird perched for extended periods and frequently darted out after passing insects. A whippoorwill (*Chordeiles* sp.) was sighted on the summit one late afternoon for one-half hour and one morning briefly. Swift lizards and horn-toad lizards were occasionally present. Crab spiders (*Misumenoides formasipes*, determined by B. Kaston) were present on the summit in curled sumac leaves in late September, 1967, and were not present in sumac bushes checked below the summit. Some of these spiders fed on hilltopping flies. Conceivably these spiders might also eat butterflies that perch on the sumac leaves, such as *Vanessa virginiensis* and *Strymon melinus*.

DISCUSSION

In this section a number of topics will be discussed in relation to hilltopping behavior in butterflies. The probable function of hilltopping in butterflies as a means of congregation to facilitate mating will be advanced, and other methods that butterflies may use to congregate for mating will be pointed out, along with some discussion of the courtship devices used. The func-

tion of territoriality in relation to hilltopping will be developed, and comparisons will be drawn between hilltopping insects and hilltopping butterflies. Special attention will be given to wind and updrafts in relation to hilltopping. In addition, possible methods of orientation in approaching summits and the extent to which hilltopping has developed in butterflies will be described.

Shepard (1966) defined a "hilltopping" butterfly as a "species which is found on a hilltop in only one stage of development [adult]; the food source of the larvae is not present; the insects are not forced there by a macro-environmental factor such as strong winds." In light of the results of the present study, this definition should be modified: *"Hilltopping" in butterflies is a phenomenon in which males and virgin or multiple-mating females instinctively seek a topographic summit to mate.* The generalized behavior pattern of hilltopping species is given in Fig. 15. Hilltopping apparently *does* occur in some species whose larval foodplants are present on or near a summit as well in species that fly to a summit a considerable distance away from the nearest foodplant. Territorial or patrol behavior at the summit is the most conspicuous aspect of the hilltopping male butterfly.

The idea that hilltopping butterflies congregate on summits for the purpose of mating is mentioned occasionally in the literature. Seitz (1909) said that the sexes in *Papilio machaon* and *P. podalirius* meet on summits for mating but did not cite supporting evidence. Moffat (1922) suspected that *Vanessa cardui* and *V. atalanta* individuals on a hilltop at Wexford, Ireland, were males; each "attacked" all newcomers "to keep the ground to himself in the hope that ultimately a female would appear." Moffat also thought that hilltopping was a peculiarity of the mating season since during a different time of the year *Vanessa* individuals were in lowlands but not on summits, while neither species was seen in the lowlands when hilltopping. (However, *V. cardui* and *V. atalanta* hilltop only in the afternoons, so that this observation was probably a reflection of the time of day rather than the time of year.) Peile (1923) noted that *Melitaea trivia persea* males in Mesopotamia frequent ridge crests; he found one pair *in copula* on a crest and concluded that ridge crests are probably their mating sites, "the males waiting there to waylay the females as they come by." Clark (1932:192) mentioned that *Papilio polyxenes asterius* mates on summits but gave no details. Temple (1953) reported that *Pararge megaera* mated after "all moved uphill to a stony arid place." Wyatt (1957a)

found two *in copula* pairs of *Papilio machaon aliaska* on a ridge summit where hilltopping males were active. Guppy (1962) concluded from observations on *Oeneis nevadensis* that hilltopping serves to bring the sexes together. He did not report any actual matings. Guppy developed certain theoretical implications of this mechanism. He pointed out that hilltopping is probably an instinct to fly to a central point in newly emerged individuals; females would lose this instinct once mated and would depart to oviposit. Natural selection would eradicate the habit if no mating occurred. An important point to stress that Guppy mentions is that females would be on summits only for the brief time to mate and thus a collector could easily miss seeing them. Emmel and Emmel (1967) reported that *Papilio indra kaibabensis* males "hilltop" on the rims of the Grand Canyon, Arizona, where presumably virgin females fly up to mate, several thousand feet higher than their nearest foodplants.

Other methods for bringing the sexes together for mating besides hilltopping probably include males flying to treetops; over rockslides; through bogs; in canyons, stream courses, and gullies; and around the larval foodplant. Jackson (1961) suspected that members of the lycaenid subgroup Lipteninae in Uganda ascend to treetops to mate since most of the females collected there had fresh wing condition. Examples of each type are given in Table 22. It remains for future investiagtion to establish the importance of these methods for mating in butterflies.

Catts, Garcia, and Poorbaugh (1965) found that males of the oestrid fly *Hypoderma lineatum* aggregate probably for mating along the open margins of streams in pastureland ravines. Certain other members of this family mate at summit congregation sites. Mating of *Sirex noctilio*, a siricid wasp, occurs on treetops where males periodically swarm (Morgan, 1968). Certain other species in this family are known to "hilltop." In moths certain members of the Lasciocampidae, Bombycidae, Saturniidae, and Arctiidae mate by the males homing in, sometimes over long distances, on a pheromone that the virgin female releases (Butler, 1967; Ewing and Manning, 1967). No such long-range method has been noted for butterflies. Certain butterfly congregations probably serve no mating function, such as male congregations for feeding (Reinthal, 1966) and butterfly migrations (Williams, 1930).

If hilltopping is a mating mechanism in insects, one would expect this behavior pattern to be developed to a greater extent

TABLE 22. Probable methods of bringing sexes together for mating in butterflies besides hilltopping

Method	Examples
1. Tree-top seeking	*Delias* spp. (Seitz, 1927:123), *Eriboea* spp., *Charaxes* spp., *Euripus consimilis*, *Euthalia garuda* (last four from Wynter-Blyth, 1957).
2. Rock-slide fliers	*Erebia magdalena*, *Chlosyne damoetas*, *Lycaena snowi*, *L. hypophlaeas*.
3. Confined to bogs	*Colias scudderi*, *Oeneis jutta* (Klots, 1951), *Boloria eunomia* (Klots, 1951), *Speyeria nokomis*, *Incisalia lanoraieensis* (Klots, 1951).
4. Canyon, gully, and stream fliers	
a. Territorial species	*Asterocampa celtis*, *Chlosyne gabbi*, *Euphydryas chalcedona* ssp., *Junonia coenia*, *Limenitis* spp., *Lycaena hermes*, *Apodemia mormo* ssp., *Lephelisca wrightii*.
b. Patrollers	*Papilio eurymedon*, *P. multicaudata*, *P. rutulus*, *Anthocaris lanceolata*, *A. sara*, *Pieris beckerii*, *Philotes sonorensis*.
5. Confined to larval foodplants (recognition of foodplant by males)	*Neophasia menapia*, *N. terlooti*, *Adelpha bredowii*, *Brephidium exilis*, *Philotes* spp., *Plebejus icarioides*, *Habrodais grunus*, *Hypaurotis crysalus*, *Mitoura gryneus*, *M. loki*, *M. siva*, *Satyrium dryope*, *S. sylvinus*, *Ochlodes yuma*, *Pseudocopaeodes eunus*.

Examples from personal experience except where otherwise noted.

in groups that are rare, parasitic, predaceous on ephemeral prey, or whose larval foodplants are scattered or rare than in common species or species that mate at the larval foodplant. Such groups are more likely to need a common meeting ground to facilitate mating. The following evidence supports this hypothesis.

1. Chapman (1954a) concludes from an insect survey of the summit of Squaw Peak in Montana that "parasitic and not usually abundant groups of insects were well represented."

2. Dodge and Seago (1954) report that flies collected by net on Georgia summits produced many undescribed or little-known species for which the females and life histories of most were unknown. Their entire net-collected Sarcophagidae represented more than 16 saprophagous species and more than 36 parasitic species.

3. Hilltop congregations are reported for all the major groups of parasitic bot flies (Catts, 1964): Cuterebridae, Gastrophilidae, Hypodermatidae, and Oestridae. Grunin (1959) points out that large concentrations of male bot flies on summits indicate the scarcity or absence of males in the surrounding territory and since bot flies generally have scattered, low density populations, these gathering points are probably mating places. A number of matings of bot flies on summits has been reported by Catts (1963, 1964).

4. Hagen (1962) summarizes the characteristics that aggregating Coccinellidae beetle species have in common; most of these congregate on some prominent object that forms a silhouette on the horizon, including peaks and hills. The species that aggregate are associated with "ephemeral" prey, chiefly aphids, and not with sessile Homoptera. Four large tribes which do not have many species that aggregate feed mostly on scale insects, mealybugs, or fungi—all sessile prey. Species that *do* aggregate in these tribes have ephemeral prey. Aphid-feeding species of Coccinellini that do not form aggregations feed mostly on colonial, arboreal, non-migrating aphids. Hagen suggests that "ephemeral" food led to the selection for long dormancy in the absence of food and for aggregation to bring the dispersed sexes together. Mating occurs mostly at these aggregation sites before the beetles disperse at the end of dormancy.

5. There is some evidence to show that rarer species of butterflies are more likely to hilltop than abundant species. J. Scott (in manuscript) collected butterflies randomly in Gregory Canyon, Boulder County, Colorado, from March to May, 1966, to see if species present that are known to hilltop were rarer than

non-hilltopping species. Using number of individuals collected per hour as an index, he found for 32 hilltopping species and 34 non-hilltopping species that hilltopping species averaged a third as abundant as non-hilltopping species. Although there was considerable overlap in the amount of abundance, the upper and lower ends of the scale differed significantly:

	Number of non-hilltopping species	Number of hilltopping species
One or more per hour	10	3
One-fourth or less per hour	11	21

Of the three most abundant hilltopping species, *Polites themistocles* and *Incisalia eryphon* apparently are only weak hilltoppers, and *Celastrina argiolus cinerea* may not hilltop as evidenced by the high percentage of mated females (see Table 15) collected by Scott, although *C. a. echo* definitely does hilltop in southern California.

Another advantage of hilltopping besides the congregation of adults that occur in low numbers or are scattered is the development of a stabilized gene pool from the centralization of isolated populations during mating (Catts, 1963).

Wind and updrafts as causative agents for hilltopping in butterflies seem unlikely for the following reasons. Some butterflies approach summits into the wind or at random angles to the wind, as well as flying with the wind. Butterflies actively seek and stay on hilltops during windless days, sometimes before updrafts would have much effect. Butterflies maintain a position on or near the summit even during fresh breezes. *Euchloe olympia* (Arnhold, 1952) and *Boloria polaris gronlandica* (Munroe, 1951) have been noted to return to summits after being blown off the tops by winds. Butterflies that are non-hilltoppers fly up-and-over the summit and show no such "staying" behavior. *Vanessa* species hilltop in the afternoons when winds would have much more effect than updrafts; these species often approached the summit into the wind as well as with the wind.

Shepard (1966) noted the behavior of hilltopping *Pieris occidentalis* males in relation to winds on Slate Peak, Washington. No specimens were seen approaching the top from the west where winds blow directly up out of the valleys. All arrived from the east slopes where winds were limited until the summit

was reached. They had to fly against the wind to reach the very summit.

Glick (1965) states that certain species of butterflies are wind-propelled by their manner of flight when flying directly into a strong wind. They keep their wings vertical and open and close them alternately to offer the least wind resistance. The butterfly is driven forward by the wind eddying against the wing under-surface.

Winds and updrafts in relation to other hilltopping insects parallel the findings with butterflies. Chapman (1954a) found on Squaw Peak, Montana, that "early morning summit activity was frequently considerable by 8:00 a.m. when updraft currents would be expected to be slight if present at all." Dodge and Seago (1954) noted summit activity of flies during moderate to strong winds. Aldrich (1915) reported that hovering bot flies actively maintain themselves on summits during strong breezes. Hurd (1920) mentioned that some beetles were carried by ascending winds and precipitated on a summit against their flight powers. However, Edwards (1956, 1957a) suggests that winds do not draw Coccinellidae beetles to summits. He mentions that they sometimes fly to and stay on summits on windless days as well as flying against the wind in approaching summits.

Chapman (1954b) noted in detail the effects of winds on the summit behavior of winged ants on Squaw Peak, Montana. Maximum numbers of ants were present on warm, calm days when updrafts would have their greatest effect. Sometimes the ants had difficulty maintaining themselves on the summit against the wind but were not noted to swarm in calm eddies present just below the summit. He states that air currents may play a role in transporting ants to summits but are not entirely responsible for summit swarms of ants. The evidence for this is that (1) ant swarms are localized to the actual summits and are not present along approaches where wind eddies exist, (2) look-out stations reporting "tens of thousands" of ants included grassy or brush and forest covered ridges and hills where thermal updrafts are not well developed, and (3) updrafts strong enough to be a transportation factor would carry ants up and away from summits.

In his study of Squaw Peak summit insects, Chapman (1954a) listed the following reasons why updrafts do not account for the presence of all insects on summits: (1) updrafts would not be symmetrical enough to concentrate insects over a peak as opposed to slightly lower points, (2) updrafts may carry insects

up and away from the peak, (3) updrafts are unlikely to be so selective for species and sex, and (4) updrafts would not account for "the continued presence of the large strong and fast fliers" which could easily leave the peak at any time.

Mani (1962) distinguished between insects actively seeking summits and insects passively transported by wind in the Himalayas. Vertical convection currents lift many insects including heavy-bodied forms up from the plains, where they are transported by upper-air winds, chilled, and dropped on snow and glaciers. Winged insects alive on summits are visitors from other biota lower down and have been observed ascending even when no updrafts are present and sometimes against prevailing winds, according to Mani.

Thermal updrafts on mountains are discussed by Malone (1951:663), Chapman (1954b), and Geiger (1965:407-408). Updrafts are most noticeable on southern slopes and are negligible on northern slopes. The are clearly defined on warm calm days. They are strongest at 20 to 40 meters above the ground where they average two to four meters per second. Updrafts are strongest in canyons and gullies and are weak on projecting ridges. In the northern Rocky Mountain region, updrafts generally start about 9:00 a.m. and continue to late afternoon. Updrafts reach their greatest intensity at one-and-one-half to two hours after maximum insolation.

Orientation flight toward the summit by both sexes in butterflies is almost certainly visually directed. Release experiments with *Papilio zelicaon* males on Dictionary Hill suggest that they can "home in" on the summit when released at various distances and directions and in various wind directions and velocities. Given a choice, male *zelicaon* could discriminate between which hilltop they were collected from and some other hilltop. When male *zelicaon* were released at considerable distances away from the hilltop, one could predict which new hilltop in the vicinity they would seek. Female *zelicaon* are probably responding like the males in seeking a summit and are not brought there by random flight because of the large numbers that are virgin and because only virgins sought the summit in a release experiment with mated and unmated females.

Certain insects are known to orient to distant objects (silhouettes) on the horizon. Iersel and Assem (1965) found that females of the wasp *Bembix rostrata* return to their nests by orienting to tree tops as far as 80 meters away on the horizon. Schneider (1962) reports that the beetle *Melolontha vulgaris*

after hibernation selects the area on the horizon with the greatest average height (hypotaxis) within a radius of about 3.2 kilometers during a spiral flight. Once the area is located, the beetles maintain a steady flight to the area, which is a forest or hill. Presumably a similar type of orientation and directional flight exists for males and virgin or multiple-mating females in hilltopping insects.

Kennedy (1939), investigating the upwind flight of the mosquito *Aedes aegypti,* found that the mosquitos maintained upwind flight orientation by visually referring to the apparent movement of the ground. In hilltopping insects, a combination of visual orientation to the ground and to the horizon would seem necessary to approach summits.

Once the summit is reached, the hilltopping butterfly begins territorial or patrolling behavior. In essence, the whole summit can be considered a macro-territory for the butterflies present, with micro-territories and patrol pathways established within this territory. Beusekom (1948) found that the female wasp *Philanthus triangulum* perceives micro-topographic landmarks in finding the nest, a behavior learned during one or more orientation flights. A similar learning process probably takes place in butterflies that establish territories on summits.

Nobel's (1939) definition of territory as "any defended area" has been applied to a wide variety of animals. Alexander (1961) points out that two phenomena are widely associated with territorial animals: (1) a tendency to stay in restricted areas, or to repeatedly return to specific areas, or both; and (2) aggressive behavior displayed toward intruding individuals. Carpenter (1958) reviewed territoriality in vertebrates — it is exhibited by fish, amphibians, reptiles, birds, and mammals. A general discussion of territoriality as it applies to insects is given by Alexander (1961:172-174) and Catts (1963:83-84). Catts (1963) states three criteria for proving the existence of territoriality in tagged male Diptera on summits: (1) the stationing of marked males at summits, (2) frequent intraspecific encounters with intruding males, and (3) diurnal permanence of male stations within a specific area. Presumably conditioning by familiarity with the microenvironment allows the male to dominate in his territory (Nice, 1941; Hinde, 1956). Possible advantages due to the spacing of a congregated, territorial male population include: (1) decreased chances of mass predation by a few predators, (2) less time spent in intraspecific aggression, (3) in-

creased frequency of male-female encounters, and (4) decreased interference to courting and mating pairs by other males (Catts, 1963; Lin, 1963). Catts (1963:83) emphasizes the need to observe marked individuals before territoriality can be shown to exist in a species.

Territorial behavior has been proven by mark-recapture methods for certain insect species. In Diptera territoriality is exhibited by the families Cuterebridae (Catts, 1963) and Oestridae (Catts, 1964). In Hymenoptera it is exhibited by Megachilidae (Jaycox, 1967) and Sphecidae (Lin, 1963). In Odonata territoriality is exhibited by certain dragonflies (Jacobs, 1955; Ito, 1960; Kormondy, 1961; Johnson, 1962b, c; Moore, 1964) and damselflies (Bick and Bick, 1963). In Orthoptera it is exhibited by Gryllidae (Alexander, 1961).

Strong circumstantial evidence for territoriality (a perch area combined with aggressive behavior in males) also exists for the following insect groups: Diptera in the families Gastrophilidae (Grunin, 1959) and Hypodermatidae (Grunin, 1959); Hymenoptera in Andrenidae (Linsley, 1958; Cazier & Linsley, 1963), Apidae (Janzen, 1964; Bennett, 1966; Cruden, 1966), and Scelionidae (Wilson, 1961); Coleoptera in the genus *Necrophorus* (Pukowski, 1933); and Odonata in dragonflies (Moore, 1952; Johnson, 1962a, 1964; Pajunen, 1962; Young, 1965) and damselflies (Bick & Bick, 1965; Bick & Sulzbach, 1966).

Strong circumstantial evidence exists for territoriality in various Lepidoptera species as well (Table 23). Ross (1963) marked males of two species of *Hamadryas* in an effort to prove or disprove territoriality in these species and found that they did not frequent definite perch areas but did display aggression. Pugnacity is known in a large number of butterfly species. Shapiro (1966) reported pugnacious males for one papilionid, two pierids, seven nymphalids, four lycaenids, and 18 hesperiid species in Delaware Valley, Pennsylvania.

Characteristically, aggressiveness, or pugnacity, of territorial male insects can be divided into four parts: (1) investigation flight toward intruders into the male's territory, followed by (2) chase of the intruder, or (3) intraspecific fight, or (4) a return to the perch area (Lin, 1963; MacNeill, 1964). Generally the male is perched, or resting, at a perch site in his territory until he investiagtes passing intruders (MacNeill, 1964). However, some species "patrol" a territory (e.g., the butterflies *Papilio thersites, Battus philenor, Anthocaris cethura*) and perch briefly

TABLE 23. Butterfly species that have territorial behavior, presumed from circumstantial evidence (perch area or site combined with aggressive behavior)

Species	Sources
PAPILIONIDAE	
Chilasa clytia	Wynter-Blyth, 1957
Papilio thersites	Shoumatoff, 1953
NYMPHALIDAE	
Apatura iris	Richards, 1927:304
Charaxes species	Van Someren, 1955; Wynter-Blyth, 1957
Eriboea species	Wynter-Blyth, 1957
Hypolimnas misippus	Stride, 1956
Lethe creola	Klots, 1951
L. portlandia	Klots, 1951
Limenitis astryanax	Shapiro, 1966
Nymphalis antiopa	Hargitt, 1915; Clark, 1937; Shapiro, 1966
Oeneis nevadensis	Guppy, 1962
Phyciodes tharos	Klots, 1951
Polygonia comma	Tietz, 1952
Vanessa gonerilla	Hudson, 1898
V. itea	Hudson, 1898
LYCAENIDAE	
Lycaena phlaeas americana	Klots, 1951
Satyrium titus	Shapiro, 1966
HERPERIIDAE	
Abantis paradisea	Van Someren, 1955
A. tettensis	Van Someren, 1955
Agathymus evansi	Roever, 1964
Atrytonopsis hianna	Shapiro, 1965
Bibasis sena	Wynter-Blyth, 1957
Coeliades forestans	Van Someren, 1955
Epargyreus clarus	Saunders, 1932
Hesperia species	MacNeill, 1964
Hesperia metea	Shapiro, 1965
Pyrgus communis	Clark, 1937
Thorybes pylades	Klots, 1951

if at all. Presumably the perched individual is conserving energy between aggressive encounters. MacNeill (1964:24) divided intruder-insects investigated by *Hesperia* into three categories on the basis of male behavior: (1) insects not of the same or a closely related species, (2) females of the same or a closely related species, and (3) males of the same or a closely related species. He found that male *Hesperia* will often investigate other butterflies and insects but would chase and fight only with males of the same or closely related species.

The primary function of territoriality in insects seems to be to increase the probability of mating (Alexander, 1961; Kormondy, 1961; Wilson, 1961; Johnson, 1962b; Catts, 1963, 1964; Cazier & Linsley, 1963; Lin, 1963; Johnson, 1964). Increased mating probability was the selective force necessary for "the origin and maintenance of territoriality" in dragonflies (Johnson, 1962b). Alexander (1961) found that territoriality in field crickets appeared in low density populations and was absent in high density populations, with both conditions producing a maximum degree of insemination of females.

Movement is necessary to elicit the courtship approach in all male butterflies that have been investigated (Marler and Hamilton, 1967:258). Some work has been done to isolate the stimuli that males are responding to. Tinbergen (1965) tested the Grayling, *Eumenis semele*, and found that bigness, darkness, nearness, and dancing activity of the moving object stimulated the male to respond. Swihart (1967) found that certain butterflies respond maximally to colors most like their wing pigmentation. In the nymphalid *Hypolimnas misippus*, the early stages of courtship are visually controlled and the later stages are probably "behavioral" and chemosensory (Stride, 1956, 1957, 1958).

Pheromones emitted by androconia hairs and scales are used by many male butterflies to stimulate the female during courtship. Families containing species with pheromones include Papilionidae, Pieridae, Nymphalidae, Lycaenidae, and Hesperiidae (Clark, 1927; Ford, 1957). The male odors are often perceptible to man, but the female "directive" odors are not and their presence is inferred from behavior (Ford, 1957).

Once the female is mated, certain barriers to further insemination may develop. Labine (1964) found that there may be a female "awareness" of the presence of a spermatophore that makes her resistant to courting males. In the butterfly genera

Parnassius, Euphydryas, Speyeria, and *Acraea,* the male secretes a plug (sphragis) on the female during copulation that helps prevent further mating (Labine, 1964). In the moth *Atteva punctella,* the presence of a spermatophore does not initiate oviposition but seems responsible for an inhibition of receptivity to males (Taylor, 1967). Various authors have noted that an ascending flight by mated females of certain species is an avoidance behavior to male courtship (e.g., Stride, 1958).

Table 2 lists species that are known to hilltop. Those species reported by Scudder (1887, 1889) and Weiss (1927, 1928) were merely listed as present on summits and thus need to be verified. The genus and species names listed were brought up to date with current nomenclature where known.

Certain genera in North America are apparently devoid of hilltopping species (list not exhaustive): *Colias, Cercyonis, Erebia, Phyciodes* (one possible exception), *Apodemia, Lephelisca, Lycaena, Philotes, Plebejus, Ochlodes, Pholisora, Pyrgus, Agathymus,* and *Megathymus.* K. Brown (in letter) says that certain members of the genus *Doxocopa* strongly hilltop in the early afternoons in Brazil. *Doxocopa* is probably congeneric with *Asterocampa,* although no members of *Asterocampa* apparently hilltop in Brazil or North America.

Table 24 lists eight North American genera that contain many hilltopping species. The genera *Erynnis* and *Hesperia* probably contain additional hilltopping species as yet unrecorded. Hilltopping genera containing certain species that weakly hilltop include *Speyeria* (except *callippe* and *egleis*), *Boloria* (except *astarte*), *Limenitis,* and *Incisalia.*

Ten of the eleven species of *Vanessa* (=*Pyrameis*) in the world are reported to hilltop (see Table 2). Only the species *samani* has not as yet been reported to hilltop. *V. cardui* is reported to hilltop in all the realms of the world except as yet in the Neotropical.

Hilltopping is widespread in butterflies both geographically and taxonomically. Representative species are present in all the geographic realms of the world (see Table 2). Tropical regions have large numbers of species which hilltop (see Van Someren, 1955; Brown, Table 2), although little work has been done to catalogue and study these. Sixteen of the 25 subfamilies of butterflies and five of the six families contain species which hilltop (Table 25). Of the nine subfamilies that are, at present, not known to hilltop, four (Baroniinae, Pseudopontiinae, Calinaginae, and Styginae) contain only one species each and the

TABLE 24. Genera from North America north of Mexico that contain many hilltopping species

Genus	Total number species	Number species known to hilltop	0/0 that are hilltopping species	Source of total species number
Papilio	15	11	73.3	Ehrlich and Ehrlich, 1961
Euchloe	3	3	100.0	"
Oeneis	10	5	50.0	"
Euphydryas	6	3	50.0	"
Vanessa	4	4	100.0	"
Erynnis	17	11	64.7	Burns, 1964
Hesperia	18	12	66.7	MacNeill, 1964
Thorybes	6	4	66.7	dos Passos, 1964

Papilio species from extreme southern Florida and southern Texas and strays were not considered. Also, *P. nitra* is here considered a hybrid form.

TABLE 25. Butterfly subfamilies in which species are known to "hilltop" * [1]

PAPILIONIDAE
- Baroniinae
- Parnassiinae
- * Papilioninae

PIERIDAE
- * Coliadinae
- * Pierinae
- Dismorphiinae
- Pseudopontiinae

NYMPHALIDAE
- Ithomiinae
- * Danainae
- * Satyrinae
- * Morphinae
- * Charaxinae
- Calinaginae
- * Nymphalinae
- * Acraeinae

LIBYTHEIDAE
- Libytheinae

LYCAENIDAE
- * Riodininae
- Styginae
- * Lycaeninae

HESPERIIDAE
- Megathyminae
- * Coeliadinae
- * Pyrrhopyginae
- * Trapezitinae
- * Pyrginae
- * Hesperiinae

[1] This subfamily classification for true butterflies (Papilionidae through Lycaenidae) follows Ehrlich (1958) and Ehrlich and Ehrlich (1967) and for skippers (Hesperiidae) follows Brues, Melander, and Carpenter (1954).

subfamily Libytheinae contains only ten species. Of the four remaining subfamilies that are not known to hilltop, Megathyminae fairly certainly does not (Roever, pers. comm.) and Parnassiinae, Dismorphiinae, and Ithomiinae have so far not been reported to do so.

The fact that most subfamilies contain species which hilltop and certain genera contain species which do strongly while other genera have species which do not or only weakly suggests that the hilltopping instinct has very likely developed independently in various groups at various times.

CONCLUSIONS

Hilltopping in butterflies is so widespread that it must serve an essential function and have survival value. This study offers the following evidence that this phenomenon serves to bring males and females together to insure fertilization and that other explanations for this behavior lack validity.

1. From many sources it is apparent that males of hilltopping species occur in far greater numbers on the summits of favorable hills than they do in the surrounding areas; therefore, some mechanism is operating to create relatively high densities of male populations, with some degree of stability, in very limited areas.

2. The summits offer little to attract the males that they could not find elsewhere in the way of nectar sources, moisture, larval foodplants around which the females might be emerging, shelter, and warmth.

3. Males on summits adopt territorial behavior including "patrolling" and aggression which are sexually oriented behavior patterns.

4. Females, however, do not remain on the summits unless they are unmated and males are absent or few in numbers. An abnormally high percentage of females captured on summits are virgin when compared to those captured elsewhere.

5. A substantial number of actual courtships and matings have been observed for two species on the summit.

6. Unmated *Papilio zelicaon* females, when released below the summit of Dictionary Hill, flew to the summit while mated females did not.

7. Male *P. zelicaon* released at various distances and directions from the hill were recaptured on the summit in such numbers that they must have "homed in."

A summary of the behavior patterns of hilltopping butterflies is given in Figure 15.

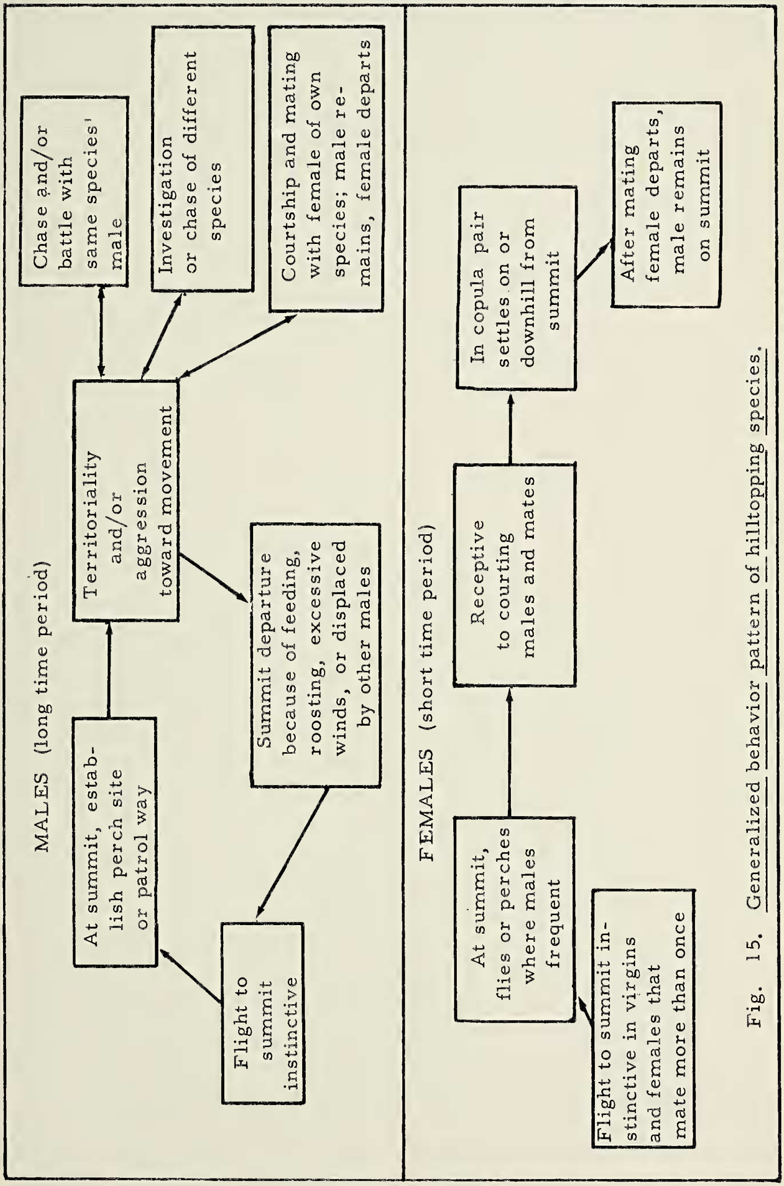

Fig. 15. Generalized behavior pattern of hilltopping species.

The urge to ascend, ascending for assemblying, tropisms, and hilltops as male playgrounds, sporting grounds, or battlegrounds can be incorporated into the broader explanation of congregation for mating. However, other possible reasons given as to why butterflies congregate at hilltops do not adequately explain the phenomenon. A male surplus on summits is a misconception since hilltops are sometimes the only place that males of certain species can be collected. Attraction to summits because of a larval foodplant availability is not always true since some species ascend far away from their foodplant area. Winds and updrafts transporting butterflies to summits is unlikely since certain species remain on summits and others fly over, since some individuals hilltop on windless days and before updrafts would have much effect, and since it is unlikely that winds and updrafts are so selective for species and sex. Wind at summits as an enticement is unlikely since species hilltop on calm days more so than on windy days.

There is much information yet to be acquired by studying hilltopping butterflies.

1. Summits are excellent places to study courtship and mating behavior of species.

2. The carrying capacity in supporting a hilltopping population needs investigation. Dethier and MacArthur (1964) demonstrated that a carrying capacity exists in the butterfly *Melitaea harrisii* by introducing a large number of larvae into a field in Maine. This effect on a summit might be tested by releasing large numbers of hilltopping butterflies in an area where they would be drawn to a hilltop.

3. The possibility that there may be a selection in territorial species for males more favorable to the species should be explored.

4. More information is needed on the apparently mild predation pressure on summits and the possibility that summit roosts offer protection from nocturnal predators.

5. Additional studies are needed to substantiate how general the phenomenon of hilltopping is on a worldwide basis.

6. The stimuli which prompt butterflies to seek summits need to be determined.

7. More work is needed in correlating rare species and species whose foodplants are widely scattered with hilltopping.

8. Further studies are indicated in the interaction between the sexes in other situations besides summits, such as males seeking tree-tops, rock-slides, bogs, canyon and gully bottoms and stream courses, and by male recognition of larval foodplants.

9. The impact of migrant species on resident hilltopping species needs to be investigated.

10. The correlation between a high percentage of virginity (i.e., lack of spermatophores in females) and hilltopping behavior should be further investigated in species in the orders suspected of this behavior.[1]

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[1] All Lepidoptera, Hymenoptera, and certain Coleoptera families form spermatophores during mating although no Diptera do (Davey, 1960).

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